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FLIGHT STRATEGIES OF MIGRATING OSPREY: FASTING VS. FORAGING

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ABSTRACT.—We developed energetics models to predict migration times and fat consumption rates of osprey (*Pandion haliaetus*) migrating south from their breeding grounds in the Intermountain West of North America. In these models we simulated three migration strategies: fasting, foraging at several mid-migration stopovers (jump strategy) and frequent foraging at stopovers (hop strategy). Because these piscivores appear to migrate predominantly over land and are rarely seen along ridges used by other migrant raptors that exploit deflection updrafts, we assumed they primarily used thermal soaring during migration. Our model predicts a 1.68-kg osprey would take 12 d and 0.25 kg of fat (a fat density of 15% of lean body mass), to complete a fasting migration of 3780 km (mean of migration distances estimated from 21 band recoveries of osprey nesting in northern Idaho and eastern Washington) when wind speed is 0 m s⁻¹. A sensitivity analysis of this model showed that changes in wind speed (± 5 m s⁻¹) had the greatest influence on migration time (8–21 d) and fat consumption (0.16–0.45 kg). In the foraging model, maximum fat deposition rate was predicted to be 0.04 kg d⁻¹. Given this prediction and assuming osprey settle for 1 d at each stopover, migrations with one, three (jump strategies), five or 11 (hop strategies) stopovers were predicted to take 17, 21, 25, or 34 d, respectively. With no settling time at stopovers the predicted foraging migration times only range from 15–17 d. The model predictions for both the foraging (without settling costs) and fasting migrations are consistent with the limited data available on fall migration strategies of osprey breeding in the Intermountain West. Our results also suggest that, under certain assumptions, nonstop migration may be energetically possible for western interior osprey.

KEY WORDS: *aerodynamic model; fat deposition; migration strategies; osprey; Pandion haliaetus; sensitivity analysis.*

Estrategias de vuelo de *Pandion haliaetus* migrantes; rapidez vs. forrajeo

RESUMEN.—Desarrollamos un modelo energético para predecir los tiempos de migración y tasas de consumo de grasas de *Pandion haliaetus* migrando hacia el sur desde sus áreas de reproducción en el oeste de Norteamérica. En estos modelos simulamos tres estrategias de migración: rapidez, forrajeo en varios sitios de descanso en el transcurso de la migración (“jump strategy”) y forrajeo frecuente en sitios de descanso (“hop strategy”). Debido a que estas aves piscívoras parecen migrar predominantemente sobre el campo y raramente son observadas a lo largo de cordones montañosos, usados por otras rapaces migratorias que explotan la deflexión de corrientes de aire, presumimos que ellas se remontan usando corrientes de aire ascendentes. Nuestro modelo predice que un individuo de esta especie de 1.68 kg podría tomar 12 días y 0.25 kg de grasa en recorrer rápidamente 3780 km (distancia migratoria media, estimada de 21 individuos marcados), cuando la velocidad del viento es de 0 m/s. Un análisis de sensibilidad del modelo mostró que cambios en la velocidad del viento (± 5 m/s) tiene gran influencia sobre el tiempo de migración (ocho a 21 días) y sobre el consumo de grasa (0.16–0.45 kg). En el modelo de forrajeo, la tasa máxima de deposición de grasa, se estimó en 0.04 kg/día. Dada esta predicción y presumiendo que *P. haliaetus* se detiene un día en cada parada, se presume que migraciones con una, tres (“jump strategies”), cinco o once paradas (“hop strategies”) toman 17, 21, 25 o 34 días, respectivamente. Sin establecerse en cada parada, el modelo de forrajeo predice tiempos de migración del rango de 15 a 17 días.

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Las predicciones del modelo tanto para la migración con forrajeo (sin costos de establecimiento) como para migraciones rápidas son consistentes con los limitados datos disponibles sobre las estrategias migracionales de otoño de *P. haliaetus* nidificantes en el oeste intermontañoso. Nuestros resultados sugieren que, bajo ciertas presunciones, la migración sin detenciones puede ser energéticamente posible para esta rapaz proveniente del oeste interior.

[Traducción de Ivan Lazo]

The migration strategies of long-distance migrants have been the focus of extensive research (see Baker 1982, Kerlinger 1989, Alerstam 1990 and Berthold 1993 for reviews), but it is still unclear whether many species of long-distance migrants make stopovers to feed during migration, rely totally on pre-migratory tissue deposition to fuel their migration, or use a combination of both strategies. Even the type of tissue accumulated for energy reserves during migration has come into question in recent years (fat vs. protein [Piersma 1990, Lindström and Piersma 1993]).

Using a bioenergetics model, Smith et al. (1986) predicted that the broad-winged hawk (*Buteo platypterus*) and the Swainson's hawk (*Buteo swainsoni*) could migrate from southern North America to northern South America (4300 km) without eating if they deposited fat amounting to 20–25% of lean body mass prior to migration. However, Smith et al. (1986) only evaluated one migration strategy (fasting). Similar to migration models developed for passerines and waders (Castro and Myers 1989, Gudmundsson et al. 1991, Lindström and Alerstam 1992), they did not conduct a sensitivity analysis of their model to evaluate the extent to which their model predictions vary with uncertainties in parameter values (see Kirkley 1991 and Goldstein and Smith 1991 for additional evaluations of the Smith et al. model).

Further insight could be provided on possible raptor migration strategies by creating models that compare fasting and foraging migration. However, the species modeled should be well-studied since empirical data are necessary for parameter estimation and for a preliminary evaluation of the realism of the model's predictions. In the United States, the osprey (*Pandion haliaetus*) is one of the few species of large raptors for which there are empirical data on its flight behavior (Kerlinger 1989), and migration distance and time (Henny and Van Velzer 1972, Melquist et al. 1978, Melquist and Johnson 1984, Poole and Agler 1987). Although there is an abundance of banding data on European osprey migrations (Österlöff 1977, Alerstam 1990), these migrations occur across large water barriers such as the Mediterranean and Baltic seas (Österlöff 1977, Alerstam 1990). These osprey use thermal

soaring over land but probably resort to flapping flight when crossing these water barriers (Kerlinger 1989, Alerstam 1990). Osprey breeding in the Intermountain West seem to migrate inland over the semi-arid southwestern United States and Central America (Henny and Van Velzer 1972, Melquist et al. 1978, Poole and Agler 1987) and probably use thermal soaring for the majority of their migration (Kerlinger 1989). We decided to model the migration strategies of osprey from the Intermountain West because the model would require fewer variables than a migration model of European osprey which would have to incorporate parameters (and assumptions) describing both thermal soaring and flapping flight.

In this paper we describe models that predict fall migration times and fat consumption rates for osprey breeding in the Intermountain West using three migration strategies: (1) fasting; (2) foraging at several mid-migration stopovers (jump strategy [Piersma 1987]); and (3) frequent foraging at stopovers (hop strategy [Piersma 1987]). We present results of a sensitivity analysis of the fasting model in which the parameter estimates were varied in a manner that reflects their empirical variation. This analysis provides insights into the key factors influencing model predictions and indicates the extent to which the model predictions vary with the uncertainties in the parameter estimates. A preliminary evaluation of the model is also presented in which we compare model predictions to empirical estimates of (1) osprey migration times from lookout observations and banding data and (2) raptor fat densities.

METHODS

Fasting Migration Model. To determine if these birds could deposit sufficient fat to fuel a fasting migration, an energetics model was constructed based on morphometrics, flight characteristics, diurnal activity patterns, energy cost of soaring flight, energy cost of roosting, and wind speed. This model assumes that fat deposits are the main source of energy during migration since there are no data available to estimate the role of other fuel resources used by osprey during migration. Values used as input parameters are shown as nominal values in Table 1. We assumed a migration distance of 3780 km. This distance is the mean of migration distances estimated from 21 band recoveries of osprey nesting in north-

ern Idaho and eastern Washington (Melquist et al. 1978, Melquist and Johnson 1984, Johnson and Melquist 1991).

Morphometric values were based on average measurements of body mass, wing span and wing area for osprey breeding in New York (Kerlinger 1989) because no comparable data sets were available for western osprey. Average mass (1.67 kg) of 33 adult osprey breeding in central Idaho (M. Bechard unpubl. data) is similar to the New York average (1.68 kg, Table 1), indicating the morphometric data on eastern osprey are a good approximation of western osprey morphometrics.

Using radar, Kerlinger (1989) measured the flight altitude of osprey using thermal soaring to migrate across central New York ($\bar{x} = 880$ m). In our model the nominal value for flight altitude was 2000 m to compensate for the increased elevation of the western migration route. Since it is difficult to determine wind velocity and direction at migration altitudes, a nominal wind speed of 0 m s^{-1} was used.

The energy cost of soaring flight and cross-country velocity were estimated with a modification of Pennycuick's model (Program 2; 1989) which is derived from theoretical aerodynamics. We chose Pennycuick's model as the template for our model because it provides the most realistic estimates of migration flight costs in comparison with other aerodynamic models (Welham 1994). Output from Pennycuick's model predicts the amount of daily fat utilized, average cross-country velocity, and daily distance flown at the predicted velocity. This model uses climb rate as an input variable for determining cross-country velocity. A climb rate of 3 m s^{-1} was chosen for these calculations, based on Kerlinger's (1989) radar-tracking results of osprey migrating in New York. This may be a conservative estimate of climb rate since thermal updrafts in the Intermountain West are exceptionally strong (Hoffman 1985). Pennycuick's model also calculates basal metabolic rate (BMR) using Lasiewski and Dawson's (1967) allometric equation for nonpasserines and then uses this estimate in the flight-cost calculations. The accuracy of allometric equations for predicting BMR of falconiformes has been questioned by several investigators (Wasser 1986, Kennedy and Gessaman 1991). Therefore, we replaced the predicted BMR in Pennycuick's model with an active phase resting metabolic rate (RMR_a) based on energetics measurements of osprey. We estimated RMR_a to be $1.24 \times \text{RMR}_r$ where RMR_r is the mean resting metabolic rate (3.69 W kg^{-1}) of three captive osprey from Florida (Wasser 1986). We increased RMR_r by 24% because active-phase measurements (RMR_a) average 24% higher than resting-phase (RMR_r) measurements in other raptors (Kennedy and Gessaman 1991).

Pennycuick's model uses these inputs of morphometrics and flight characteristics to calculate glide superpolar (GSP [dimensionless]), which describes the relationship between gliding sink speed and air speed, and interthermal velocity (V_{it} [m s^{-1}]). V_{it} is the velocity the osprey travels gliding between thermals. Pennycuick's model provides two estimates of V_{it} : V_{opt} (m s^{-1}) and V_{bg} (m s^{-1}). V_{opt} is optimal interthermal speed which maximizes distance traveled per unit time, and V_{bg} is a slower interthermal speed which maximizes glide distance. Interthermal velocities of osprey migrating in central New York (Kerlinger 1989) suggest they use an interthermal speed approximately $1\text{--}2 \text{ m s}^{-1}$ less than V_{opt} . This would allow them to migrate faster than if they chose V_{bg} , while

still allowing them to glide farther and take advantage of stronger thermals than if they chose V_{opt} . Therefore, cross-country air speed of the osprey [V_{xc} , (m s^{-1})] was calculated using an interthermal velocity that was 2 m s^{-1} less than V_{opt} estimated by Pennycuick's model.

Daily distance traveled (DDT [km d^{-1}]) was calculated as:

$$\text{DDT} = V_{xc} \times T_f \times (.001 \text{ km m}^{-1}),$$

where T_f is daily flight time in sec. Daily fat consumed in flight (FFC [kg d^{-1}]) was calculated as:

$$\text{FFC} = (2\text{RMR}_a \times T_f) / e,$$

where RMR_a is in Watts and e is the energy content of fat ($3.96 \times 10^7 \text{ J kg}^{-1}$ [Robbins 1993]). Although energetic costs are usually calculated from lean body mass because fat is relatively inert metabolically (Luke and Schoeller 1992), stored fat was included in these calculations of RMR_a to account for the cost of increased wing loading due to pre-migratory fat deposits. The amount of fat deposited for a 3780 km migration is unknown, so the model was initiated with a body mass $50\% > 1.68 \text{ kg}$. We used $2 \times \text{RMR}_a$ as a nominal estimate of the cost of gliding flight (Baudinette and Schmidt-Nielsen 1974).

As in Smith et al.'s (1986) model, we assumed that fasting osprey engage in only two activities during migration, soaring flight (8 hr d^{-1}) and roosting (16 hr d^{-1}). A daily flight time of 8 hr was used as the nominal value in this model because this approximates the length of time convective fields used by migrating, soaring hawks are available in temperate latitudes (Kerlinger 1989). From this, daily fat consumed during roosting (RFC [kg d^{-1}]) can be calculated as:

$$\text{RFC} = (\text{RMR}_r \times T_r) / e,$$

where T_r is the daily roosting time in sec. In this equation, RMR_r (Watts) is calculated from the unadjusted mass (1.68 kg) which is assumed to be a good approximation of lean body mass (M). The sum of FFC and RFC is the daily fat consumed (DFC [kg d^{-1}]).

The model was run iteratively, with DFC subtracted from initial body mass after each iteration (one day of migration). The program terminated when the new mass was $< 1.68 \text{ kg}$. Using the daily output, DDT, DFC and the number of iterations were individually summed from the termination point until the sum of $\text{DDT} = 3780 \text{ km}$. The sums of DFC and the number of iterations were used as the predictions for total fat consumed and total migration time, respectively.

Sensitivity Analysis of the Fasting Model. We compared changes in predicted migration times and fat consumed under fasting conditions to uncertainties in the following model parameters: lean body mass, wingspan, wing area, wind speed, climb, altitude, daily flight time, total migration distance, RMR_r , and the energetic cost of gliding flight (Table 1). We were interested in discovering how robust the model predictions were to uncertainties inherent in these parameter estimates and thus, identify those parameters that must be carefully estimated empirically in future research.

Parameter uncertainties were estimated by assigning upper and lower parameter bounds and running the model separately varying one parameter at a time to its upper or lower bound (Table 1). The bounds for morphometric parameter values were based on ranges of measurements of western

Table 1. Results of the sensitivity analyses of all the parameters included in the fasting model for migrating osprey. Nominal and boundary values are presented.

PARAMETER (UNITS)	NOMINAL	RANGE	MIGRATION TIME (d)	FAT CONSUMED (g) (% FAT DENSITY)
Lean mass (kg) ^a	1.68	1.35–2.03	12–13	196(14)–293(14)
Wing area (m ²) ^a	0.30	0.24–0.33	12	239(14)–248(15)
Wing span (m) ^a	1.49	1.34–1.58	12	243(14)–247(15)
Altitude (m) ^b	2000	1000–3000	12	240(14)–249(15)
Climb (m s ^{−1}) ^c	3	2.5–3.5	11–13	225(13)–267(16)
Wind speed (m s ^{−1}) ^d	0	−5.0–+5.0	8–21	164(10)–447(27)
Flight time (hr d ^{−1}) ^b	8	6–10	10–16	205(12)–284(17)
Migration distance (km) ^e	3780	2940–4620	9–15	185(11)–304(18)
RMR (W) ^f	6.2	4.0–6.2	12	163(10)–247(15)
Cost of flight (×RMR _a) ^g	2	2–4.5	12	247(15)–416(25)

^a Nominal value from Kerlinger (1989) and bounds are from M. Bechard (unpubl. data).
^b Estimated value (see text).
^c Nominal value from Kerlinger et al. (1985 in Kerlinger 1989). Bounds were based on climb rates observed in other soaring hawks by Kerlinger et al. (1985 in Kerlinger 1989).
^d Estimated value (see text). Positive values indicate a head wind and negative values indicate a tail wind.
^e Nominal value is the mean of 21 band recovery distances from osprey breeding in the Intermountain West (Melquist et al. 1978, Melquist and Johnson 1984, Johnson and Melquist 1991). Upper and lower bounds are ±1 SD.
^f Nominal value is the average resting metabolic rate (RMR) measured for three captive osprey during their resting phase (Wasser 1986). The lower bound is based on Wasser's allometric equation for estimating RMR for Falconiformes during their active phase. The nominal value was also used as the upper bound because these measurements are higher than predicted by any published allometric equation for estimating RMR for nonpasserines during their active phase.
^g Values are based on Baudinette and Schmidt-Nielsen's (1974) measurements of energetic costs of gliding flight in herring gulls (*Larus argentatus*). The lower bound is based on the measured difference between resting metabolic rate and gliding metabolic rate in the wind tunnel. The upper bound is the difference between the measured gliding metabolic rate and the resting metabolic rate calculated using Lasiewski and Dawson's (1967) equation for nonpasserines. The lower bound was used for the nominal value since metabolic rate during flight was calculated using active phase RMR.

osprey (M. Bechard unpubl. data). Bounds for the flight characteristics and wind speed were based on published variations of these parameters for migrating osprey or other large migrating raptors if data on osprey were not available (Kerlinger 1989, Kerlinger and Moore 1989). The nominal value for RMR_r was used as its upper bound because Wasser's (1986) metabolic measurements on osprey were higher than the predictions from allometric equations. The lower bound for RMR_r was estimated with Wasser's (1986) equation for resting phase RMR_r in falconiformes. This equation predicts lower values for RMR_r than do the equivalent allometric equations for nonpasserines (Aschoff and Pohl 1970, Lasiewski and Dawson 1967).

Foraging Migration Models. If these osprey chose not to fast during the entire migration, they would have to spend time foraging daily or break up their trip into several segments that are separated by stopovers to replenish their fat reserves. To compare fasting migration to foraging migration, the fasting model was modified to estimate total migration time and stopover fat deposition for jump or hop strategies (Piersma 1987). Migration models using the jump strategy included migrations with one stopover (after 1890 km) and three stopovers (one every 945 km), while the hop strategy included five stopovers (one every 630 km) and 11 stopovers (one every 315 km—the daily flight distance predicted by the foraging model).

To estimate fat-deposition rates at stopovers, maximum daily fat deposition rate (FDR_{max}) was calculated using Lindström's (1991) Eq. 1:

$$FDR_{max} = \frac{(DME_{max} - DEE_{min})}{M} \times \frac{(100 n)}{E},$$

where FDR_{max} is a percentage of lean body mass, DME_{max} is maximum daily metabolizable energy intake in kJ, DEE_{min} is minimum daily energy expenditure in kJ, M is lean body mass in kilograms, n is the conversion efficiency of metabolized energy into fat (0.88 [Kersten and Piersma 1987]), and E is the energy content of stored fat (3.96 × 10⁴ kJ kg^{−1}). Like Lindström, DME_{max} was calculated using Kirkwood's (1983) allometric equation; however we calculated DEE_{min} as:

$$DEE_{min} = DEE + (DME_{max} \times 1\%), \quad (\text{Eq. 1})$$

where DEE is the minimum daily energy expenditure of 1.5 BMR predicted by Lindström (1991). The additional term in Eq. 1 (DME_{max} × 1%) estimates the additional energy expenditures incurred by hunting osprey (kJ d^{−1}) (Machmer and Ydenberg 1990).

Lindström and Alerstam (1992) observed that birds at stopover sites lose body mass during the first day at the site and/or there is a time lag before fat deposition starts, but Moore and Kerlinger (1987) found that weight gain can

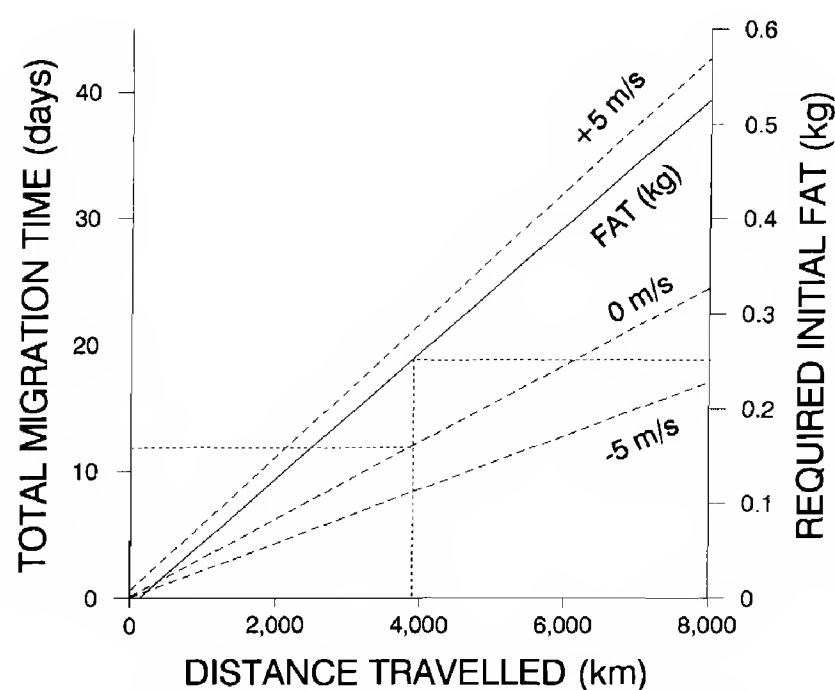


Figure 1. Fasting model predictions of total migration time at three different wind speeds (dashed lines) and required initial fat deposits (solid line) for an osprey breeding in the Intermountain West to complete a 3780 km southward migration. The dotted lines to the X and Y axes indicate the predicted duration and amount of premigratory fat deposition for migrations under nominal conditions.

occur on their arrival day at a stopover. Therefore, we evaluated the foraging migration using three stopover strategies: (1) stopovers with one day of settling before weight gain begins; (2) stopovers with weight gain beginning on the first day of stopover; and (3) foraging daily without stopovers. In the first strategy we assumed (1) osprey's energy expenditures while settling were equal to DEE and (2) they arrived at stopovers with enough fat to spend one day without foraging.

RESULTS

Fasting-model Predictions. Fasting-model predictions are summarized in Fig. 1. The solid line in Fig. 1 represents model predictions for total fat consumption using nominal values listed in Table 1. Dashed lines are model predictions for distance traveled with the nominal value and the lower and upper bounds for wind speed. As indicated by the dotted lines in Fig. 1, we predict that a 1.68-kg osprey would take 12 d, consume 0.25 kg of fat (a fat density of 15% of lean body weight), to complete a fasting migration of 3780 km if it migrated with no head or tail wind.

Sensitivity Analysis of Fasting Model. The results of the sensitivity analysis of the fasting model are listed in Table 1. Variation in wind speed caused the greatest change in predicted fat consumption and migration time, with a 3780 km migration taking 21 d and 0.45 kg of fat (27% fat density) in a 5 m s^{-1} head wind, or 8 d and 0.16 kg of fat (10% fat density) in a 5 m s^{-1}

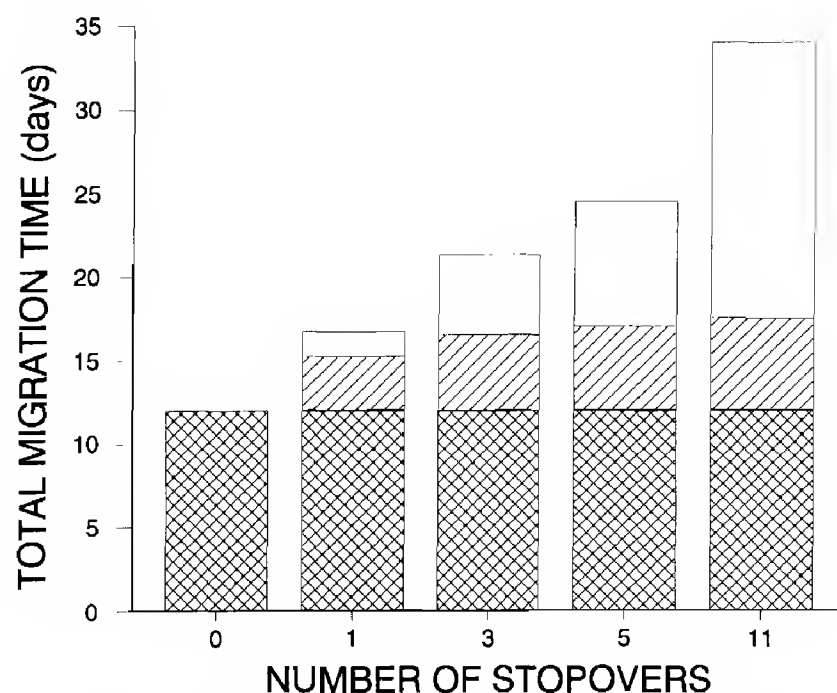


Figure 2. Foraging model predictions of total migration time with zero, one, three, five or 11 stopovers. The cross-hatched portion of each bar indicates the predicted time in flight, the hatched portion indicates the predicted total time foraging at stopovers, and the unshaded portion indicates the predicted total settling costs (time spent settling at stopovers [1 d stopover⁻¹] plus the extra time spent foraging to cover the energy expenditures of the days settling at stopovers). If there are no settling costs, then the total migration time is represented by the sum of the cross-hatched and hatched portions of the bar.

tail wind (Fig. 1). The amount of time a bird flies during the day and total distance migrated also resulted in large changes in model predictions. Flying 6 hr d^{-1} would increase migration time 33% and fat consumed 13%, while changing flight time to 10 h d^{-1} reduces the predicted migration time by 17% and fat consumed by 17%. An 840-km variation in migration distance changed migration time by 25% and fat consumed by 23–25%. Uncertainties associated with estimates of RMR and energetic cost of flight did not change the predicted migration time but did vary the predicted fat consumed by as much as 34% and 68%, respectively. Uncertainties associated with the other parameters caused predicted migration times to vary by no more than 1 d and predicted fat density to vary by only 1–2%.

Foraging-model Predictions. We estimate maximum daily fat deposition rate (FDR_{max}) to be 2.2% (0.04 kg d^{-1}) and that it would take 7 d of maximum energy intake to deposit a premigratory fat density of 15% of lean body mass (predicted fat density for a fasting migration of 3780 km). In comparison, based on Lindström's Eq. 1 (1991) and Lasiewski and Daw-

son's (1967) allometric Eq. E for estimating passerine BMR, a 0.015-kg passerine would require only 2 d of maximum energy intake to deposit a comparable premigratory fat density. Using Machmer and Ydenberg's (1990) estimates of 218 kJ average net energy gain per prey, an osprey would require 11 fish per d, or a total of 77 fish, to provide the fat stores required for a 3780 km fasting migration. The addition of stopovers to the migration would increase the predicted time investment to 15, 16, 17, and 18 d with one, three, five, and 11 stopovers, respectively (Fig. 2). However, if there is settling time at each stopover, the total migration time is predicted to increase to 17, 21, 25, and 34 d, respectively.

Model Evaluation. Although premigratory fat densities are not available for osprey, the predicted fat density of 15% is very close to the maximum fat density measured in comparably sized European goshawks (*Accipiter gentilis*) (16.4% in a 1.67-kg female, Marcström and Kenward 1980). This fat density prediction is also well below the premigratory fat densities that have been observed in warblers and waders (>50%, Blem 1980), and the predicted fat densities of migrating buteos (Smith et al. 1986). American kestrels (*Falco sparverius*) were found to have fall fat densities 2–4% higher than mid-summer values (5.3–7%, Gessaman 1979), but Kirkley and Jones (unpubl. data) point out that these fat levels are not maximal, and should be considered wintering fat since they are maintained throughout the winter. Obviously, more quantitative data on premigratory fat deposition in raptors will be necessary to determine if the fat deposition patterns predicted by this model occur in nature.

Based on the disappearance of resident birds from nesting territories, osprey migrations in northern Idaho begin as early as the first week of September (Melquist et al. 1978, Melquist and Johnson 1984). Peak numbers of osprey counted at a migration station in northern Utah occur during the second and third week of September (Hoffman 1990). Osprey from the Intermountain West are widespread in Mexico by late September (Melquist and Johnson 1984), with banded first-year migrants recovered in central Mexico as early as 17 September (2700 km from banding site [Melquist and Johnson 1984]) and adults recovered as early as 28 September even further south (4200 km from banding site [Melquist and Johnson 1984]). Osprey banded as nestlings from 14 July to 2 August were recovered 46–135 d later, after travelling a maximum of 3500 km from the banding site (Melquist and Johnson 1984). The predicted travel time of 12 d for a fasting migration

with no head wind is much less than the shortest times observed between banding and recovery, but may be comparable to actual migration times if osprey leaving Idaho in the beginning of September arrive in central Mexico by mid-September.

The model's prediction of 21 d for a fasting migration with a 5 m s^{-1} head wind is comparable to empirical estimates of migration times, but the predicted fat density of 27% is much higher than measured fat densities in raptors. These predictions suggest that osprey from the Intermountain West probably do not migrate entirely into head winds of this intensity. There are no observations of wind conditions along osprey migration routes in the Intermountain West to evaluate our conclusion. However, observations by Hall et al. (1992) demonstrate that significantly more coastal migrants in California migrate south with no wind or tail winds than with head winds.

The addition of five or more stopovers with settling costs increased the total migration time to 25–34 d (Fig. 2), which is 2–3 times the predicted migration time while fasting and slightly longer than the empirical migration time estimates based on band recoveries. With one or three stopovers, the predicted total migration time is 17 or 21 d, respectively (including settling costs). It seems unlikely that osprey would make frequent foraging stops that included a day of settling and a day of foraging. Settling times are mostly observed in territorial migrants that travel in large, intraspecific flocks (Lindström and Alerstam 1992). Because osprey migrate individually or in small flocks (Kerlinger 1989), it is possible they do not experience settling costs. Without settling costs the total migration time with multiple stopovers is predicted to be 15–18 d (Fig. 2).

Without these settling costs, frequent foraging throughout migration could occur with little affect on migration time if osprey foraged and flew in the same day. Although a 1.68-kg osprey may only be able to metabolize 11 fish d^{-1} , it may not take them a whole day to catch those fish. Osprey have one of the highest capture success rates of any raptor (Newton 1979). Swenson (1978) observed average fish catch rates for osprey to be 8.8–19.7 min fish^{-1} , and Machmer and Ydenberg (1990) observed an average of 10.3 min fish^{-1} . Therefore, with good forage availability, an osprey may require <2 hr to catch its metabolic maximum. Alternatively, osprey may only need about five fish d^{-1} , or 45–100 min of daily foraging, if their strategy is to cover the costs of a single migration day and not deposit fat for subsequent days. If there are

adequate water sources en route, e.g., reservoirs and lakes, it is possible that an osprey could forage daily without affecting its daily time in flight and total migration time by hunting at the beginning or end of each day before the thermals were strong enough for soaring.

CONCLUSIONS

Our foraging- (without settling costs) and fasting-model predictions are consistent with the limited data available on fall migration strategies of osprey breeding in the Intermountain West. Our results also suggest that, under certain assumptions, nonstop migration may be energetically possible for western interior osprey. Whether or not stopovers are used by these osprey is probably a function of the food availability en route. Hop strategies are generally thought to be the most favorable for conserving energy (Piersma 1987) but probably require plentiful food resources en route. In ecologically unfavorable situations, e.g., low food availability, fasting or jump strategies are more likely (Johnson and Herter 1990, Berthold 1993). Anecdotal observations of osprey carrying fish during migration (Kerlinger 1989) combined with few foraging areas in the semi-arid Southwest and Mexico would suggest a jump strategy as the best strategy for osprey migrating from the Intermountain West.

Although our predictions are consistent with empirical observations, our model was not evaluated rigorously because of the absence of observations on migration strategies of individual osprey. Programmable satellite transmitters are now available that are small enough (<30 g) for medium to large raptors, which allow investigators to measure migration and stopover times, and identify migration routes of individual birds (R.E. Ambrose, M.W. Britten, P. Howie and P.L. Kennedy unpubl. data). This new technology can also be used to measure the daily time in flight, a key parameter in our model. Based on our sensitivity analysis, precise estimates of wind speeds at the location of a bird in flight are also necessary for accurate predictions, but this type of information will probably not be available until anemometers can be attached to the satellite transmitters. Anemometers on osprey would measure airspeed moving past the bird (V_a) while the satellite transmitter would indicate changes in location, allowing the calculation of ground speed (V_g). $V_g - V_a$ could be used as an estimate of the wind velocity between migration locations.

Empirical data on premigratory and stopover fat deposition (if any) by migrating osprey are also needed

to determine if this model adequately presents the major factors influencing fat deposition strategies. Total body electrical conductivity (TOBEC) has been used to estimate fat in live animals. However, a recent evaluation of this methodology by Skagen et al. (1993) indicates TOBEC accurately measures lean body mass but its lipid estimates have numerous potential errors. Other technologies are being evaluated to estimate lipids of free-ranging animals in a non-invasive manner (J.A. Gessaman pers. comm.). With these new technologies, osprey migration strategies can be determined empirically and these data can be used to evaluate the validity of our models.

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BEHAVIOR OF PEREGRINES IN WINTER IN SOUTH TEXAS

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ABSTRACT.—The movements and other behaviors of seven radio-tagged peregrine falcons (*Falco peregrinus*) were determined in winter near the Laguna Madre in southern Texas in 1993 and 1994. In January and February most of the falcons hunted in areas 20–28 km across and showed extensive overlap. Most locations of falcons we monitored were on the vast tidal flats at the margins of the Laguna or over the shallow water where numerous perches are present in an otherwise featureless habitat. One adult female moved a maximum of less than 8 km. Four of the falcons we instrumented had been trapped in the area before, or remained months after the study. We estimated a minimum density of 20 peregrines inland of the beaches of South Padre Island, or about one bird per 50 km². The Gulf Coast of Texas and Mexico have several times the area of tidal flats we observed and the region is surely a major newly discovered wintering area for peregrines. We speculate that some peregrines may spend their first summer there.

KEY WORDS: *behavior; peregrine; radiotelemetry; Texas; winter dispersion.*

Conducta de *Falco peregrinus* durante el invierno en el sur de Texas

RESUMEN.—En el invierno de 1993 y 1994 se determinaron los movimientos y otras conductas de siete individuos de *Falco peregrinus* radiomarcados, cerca de Laguna Madre en el sur de Texas. En enero y febrero la mayoría de los individuos capturados en áreas de 20 a 28 km de largo mostraron gran sobreposición. Estimamos que la mayoría de las localizaciones de halcones se realizaron sobre un vasto plano de mareas en el margen de la Laguna o sobre aguas poco profundas, donde numerosas perchas están presentes. Una hembra adulta tuvo un máximo de dispersión de menos de ocho km. Cuatro de los halcones instrumentados fueron capturados en el área o permanecieron meses después del estudio. Estimamos una densidad mínima de 20 halcones peregrinos al interior de las playas del Golfo de South Padre Island o cerca de un ave por km². Las Costas del Golfo de Texas y México parece ser una gran área invernal para halcones peregrinos. Especulamos que algunos individuos pasan su primer verano en este lugar.

[Traducción de Ivan Lazo]

Peregrine falcons (*Falco peregrinus*) have been studied in migration on the coast of Texas, in fall (Hunt et al. 1975) and in spring (Hunt and Ward 1988). Band recovery data indicated the migrants originated in the Arctic and wintered in Central and South America (Yates et al. 1988). Examination of winter band recoveries and Christmas Bird Counts from the coast of the Gulf of Mexico suggested the possibility of a substantial population (Enderson 1965). Sightings in winter near Brownsville, Texas, by L. Meredith (pers. comm.) in the 1950s and discovery of many peregrines on the Culiacán Marsh on the Sinaloa coast in western Mexico (Enderson et al. 1991) prompted us to search for peregrines in winter at about the same latitude in southern Texas. We report here on the behavior of winter resident peregrines determined by telemetry, estimate the area population, and speculate on the possibility that per-

egrines are present year-round on the coast of the Gulf of Mexico.

STUDY AREA AND METHODS

We searched for peregrines on South Padre Island (SPI) south of the Mansfield Channel and the adjacent mainland (Fig. 1) from 9 January to 8 February 1993 and 1994. Searches on the island were made from dunes near the beach and by all-terrain vehicles on the vast leeward tidal flats. On the mainland we traveled the tidal flats adjacent to the Laguna Madre. We used a boat, airboat, and an airplane four times to visually verify the locations of birds on the Laguna. Trapping was done with rock doves (*Columba livia*) in noose-covered harnesses and radios were mounted on the two central rectrices as described in Enderson et al. (1991). We searched for all instrumented peregrines as weather permitted, roughly dividing our effort between island and mainland on alternate days.

Positions of instrumented falcons were determined by following radio signals to their sources or by triangulation of two simultaneous bearings taken from the 10 tallest

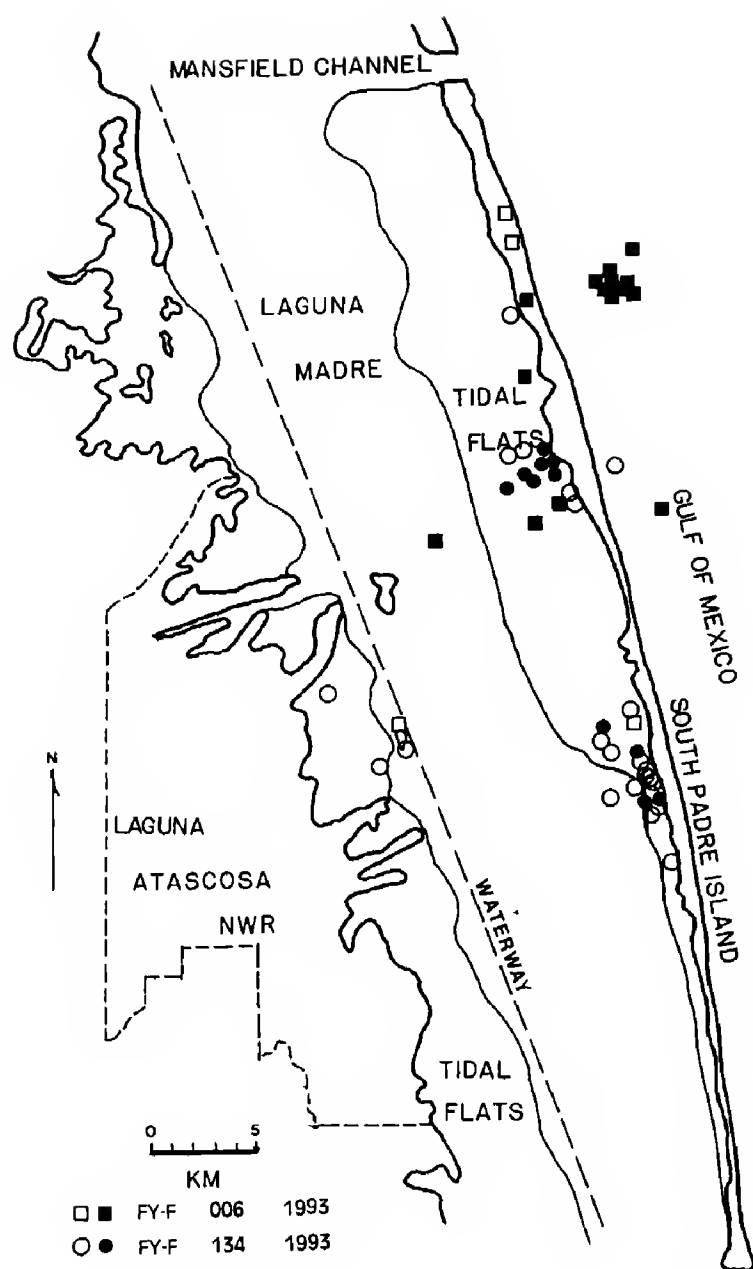


Figure 1. Locations of first-year peregrines in 1993. Open symbols are visual locations, closed symbols are telemetry triangulation locations; none are <1 hr apart, and were made over 20 d (006) or 32 d (134), January to February.

dunes along the northern 35.2 km of the island. We used dunes at least 4 km apart while obtaining bearings on signals. Maximum reception range from dunes was 10–15 km depending on the elevation of the falcon. On the mainland we used the highest points available for receivers, often dirt banks on islands overlooking vast tidal flats and the Laguna Madre. Receiver locations were determined by a geographical positioning system and verified on 7.5 min topographical maps. The great majority of fixes on transmitters were at distances less than 10 km because of the narrowness of SPI. When a signal was obtained we took fixes every 15 min in 1993 and every 30 min in 1994. When falcons were in motion we often tracked them continuously. Because several birds were instrumented in the same period and searches for lost birds were necessary, we could not always track each bird all day. We tracked each bird from dawn to dusk at least four times to learn its activity patterns. We often attempted to locate individuals visually, especially in 1993.

We tested telemetry accuracy by attaching three trans-

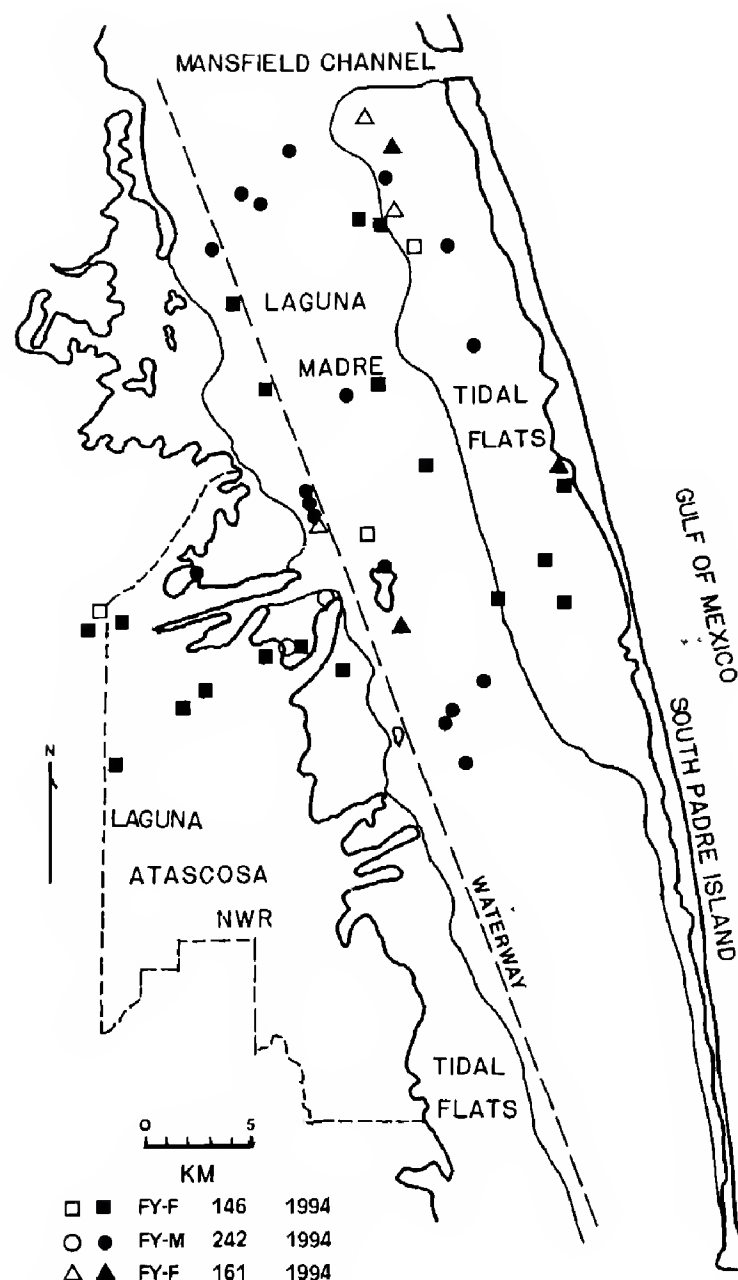


Figure 2. Locations of first-year peregrines in 1994. Open symbols are visual locations, closed symbols are telemetry triangulation locations; none are <1 hr apart and were made over a period of at least 17 d (161).

mitters to fence posts and recording the degrees of error from true bearing from eight receiver locations 2.3–3.5 km away. The mean error of 40 trials was 2 degrees (range = 0–5 degrees; SD = 1.21 degrees). Under usual field conditions that average error could yield a maximum triangulation error of 1.5 km if the transmitter were 8 km from the two receivers and lateral to the midpoint of a line between them. If one standard deviation is added in the above example the error would be 3.2 degrees and a maximum error of 2.5 km in position would result. Actual error is dependent on the geometry of transmitter and receivers, and on the combination of bearing errors. Because 73% of our test bearings were less than two degrees of true bearing, 2 km was probably a conservative estimate of the maximum error, but a few estimates could be in error by twice that distance or more.

We minimized autocorrelation between sequential positions by dividing the total time each falcon was observed by the number of times the falcon flew to a different position. The average time between movements for all

Table 1. Observation periods and success in obtaining visual and telemetry locations for peregrines in winter in the Laguna Madre area of southern Texas, 1993–94. Accepted locations were separated by at least 1 hr.

YEAR/ INDI- VIDUAL	AGE ^a	SEX	OBSERVA- TION PERIOD (d)	DAYS LOCATED	ACCEPTED LOCATIONS VISUAL ^b — RADIO	LOC. < 120 MIN APART	MEAN NO. LOCATIONS PER DAY	EST. MAX. DIST. ^d (km)
1993								
115	ASY	F	27	16	30—4	3	2.1	7.5
006	FY	F	20	7	15—4	7	2.7	24.5
134	FY	F	32	17	24—11	4	2.0	26.5
1994								
034	ASY	F	25	17	8—33	9	2.4	20.0
202 ^c	SY	F	24	12	3—17	3	1.7	20.0
242	FY	M	26	9	2—17	0	3.1	28.2
161	FY	F	17	5	3—3	1	1.2	23.7
146	FY	F	27	11	3—18	2	1.9	28.0

^a FY = first year, SY = second year, ASY = after second year.
^b Includes the trapping event.
^c Same bird as 134 in 1993.
^d Distance between most distant locations for each peregrine.

falcons was 48 min (SD = 19 min). To facilitate data selection we therefore accepted only visual or triangulation locations separated by at least 1 hr.

RESULTS

We instrumented seven peregrines, one of which (134/202) was tracked in both years (Table 1). Trapping began 9 January each year and the latest any bird was caught was 19 January (006 in 1993). Sometimes several accepted locations were obtained per day, but the daily average for each bird was about three or fewer. Further, the majority of locations we accepted were separated by more than 2 hr (Table 1).

Movements and Dispersion. With one exception, instrumented peregrines were located both on SPI and on the mainland (Figs. 1–3). In general the falcons moved widely from the coastal region just inland from the beaches on the gulf westward to the margin of pastures and brushlands on the mainland. The exception was adult female 115 which was very sedentary on tidal flats adjacent to Laguna Atascosa National Wildlife Refuge (Fig. 3). The corridor of suitable habitat east to west is about 20 km wide in this region, corresponding roughly to the maximum spread of locations we found for these birds (Table 1). The north to south spread of locations for first-year peregrines on the Laguna was about the same distance as their east to west range.

About 115 of the 198 locations (58%) of peregrines shown on Figs. 1–3 were on island and mainland tidal flats. Another 53 locations (27%) were on the open water of the Laguna Madre where numerous perches were available. Remaining locations were on the mainland, island dunes, or on the gulf.

Immature peregrine 006 was banded in Greenland in 1993 and we found that she frequented the northern half of SPI and off-shore oil drilling towers (Fig. 1). Her observed range overlapped extensively with another first-year female (134) and had a similar maximum extent. Female 134 had been banded in late October 1992 on SPI by other workers (T. Maechtle pers. comm.).

In 1994, the movements of first-year peregrines 146 and 242 were best recorded; they moved between island and mainland several times and their positions were unpredictable (Fig. 2). Both were found on the Laguna Madre where dredge spoilings along the waterway or numerous stilt shacks, posts, markers, or wrecked boats provided perches.

An adult female (115) in 1993, adult female 034 in 1994, and the second-year female 202 in 1994, showed less dispersion in most of their estimated locations than did the first-year falcons (Fig. 3). Adult 115 was most predictable and sedentary (Table 1). We watched her with binoculars a total of 40 hr from 13 January to 8 February and she usually

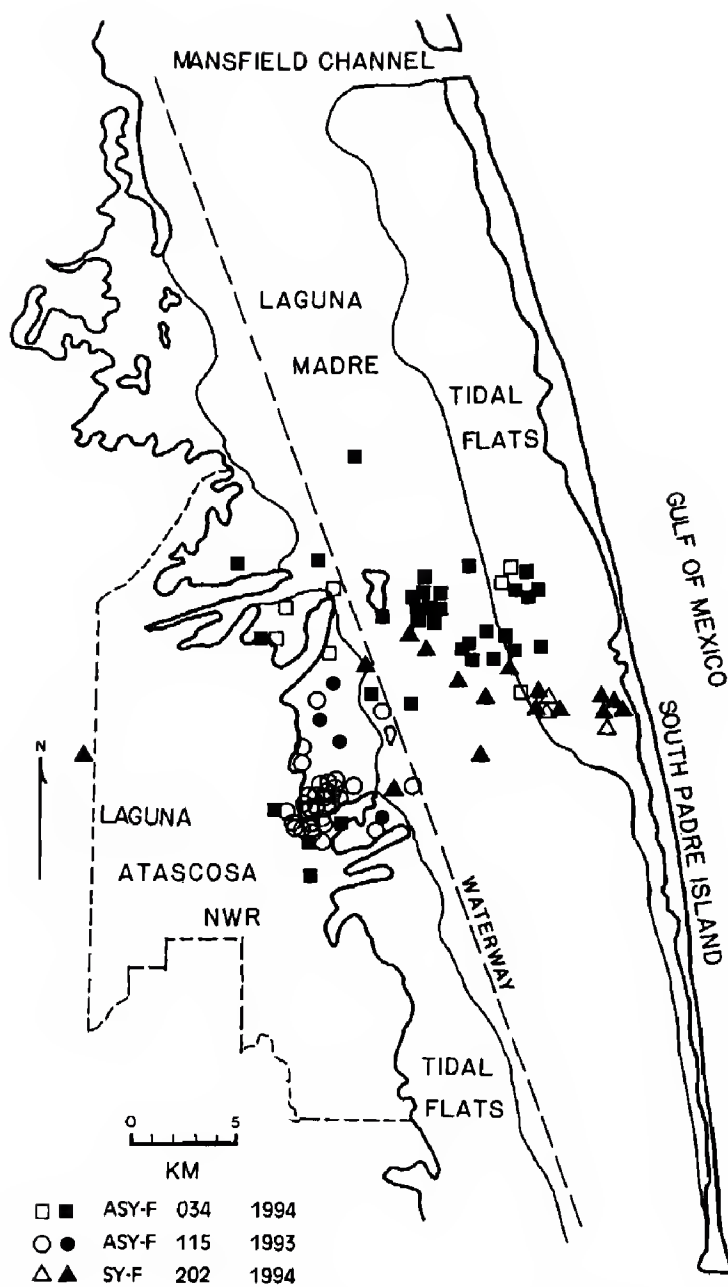


Figure 3. Locations of a second-year and adult peregrines in 1994 and 1993. Open symbols are visual locations, closed symbols are telemetry triangulation locations; none are <1 hr apart and all span at least 24 d (202).

perched within 300 m of a small lake used by hundreds of ducks.

Two falcons tracked in 1994 were retrapped by other workers 4 mo later on SPI tidal flats (T. Maechtle pers. comm.). Second-year female 134/202 was caught, her transmitter was removed, and she was released 11 April 1994 within 3 km of locations where radios were attached in 1993 and 1994. Female 134/202 had been banded on SPI in late October 1992 when only a few months old and may have spent much of her life on SPI. First-year female 161 was retrapped 12 April 1994 about 14 km south of Mansfield Channel on SPI (Fig. 2). Adult female 034, tracked in 1994 (Fig. 3) had been trapped on SPI in October 1990, and again in 1993 (T. Maechtle pers. comm.).

Population Estimate in 1994. In addition to the five falcons instrumented, we trapped a first-year female whose transmitter failed soon after release, and we saw many other peregrines. Two adult females roosted repeatedly on buildings in the town of South Padre Island and three first-year females, presumed to be different individuals, were on the refuge. In 1994, an adult female was seen nine times on the same perches used by 115 in 1993; we believe it may have been the same bird. Another especially dark-headed female was seen seven times 4 km south of the previous adult, and another adult was seen four times 10 km north of the apparently returning adult. Another adult female was seen several times on markers on the Mansfield Channel, and four more adults, apparently distinct from all those above, were seen on markers on the Intercoastal Waterway between the Refuge and the Channel.

If these sets of sightings were of different individuals, a minimum of eight adults occurred along the waterway, two in town, one on the Channel, and the two we tagged, yielding a total of 13. In addition to the three first-year peregrines we tagged, one with the broken transmitter was on SPI, and probably three additional individuals on the refuge, resulting in a minimum of seven first-year birds. By conservative estimate, there were about 20 individuals in the study area of about 1000 km², or about one bird per 50 km².

Interaction and Food. In both years we saw six instances of adult peregrines attacking conspecifics, both adults and first-year birds. One of the latter was chased by an adult about 1 km from SPI over the gulf, and another adult left a perch on a mainland tidal flat to chase another adult soaring about 2 km away. All attacks were vigorously aggressive resulting in the rapid departure of the attacked bird. However, twice adults did not chase nearby conspecifics.

We saw adult peregrines chase a ferruginous hawk (*Buteo regalis*), a northern harrier (*Circus cyaneus*), an osprey (*Pandion haliaetus*), and a turkey vulture (*Cathartes aura*). In a fourth incident, a vulture pirated a dead rock dove from a first-year peregrine by shuffling closer, side-stepping almost imperceptibly, until the feeding falcon was slowly forced to leave its prey in the shadow of the seemingly indifferent vulture. The vulture then fed on the pigeon.

Prey. We saw peregrines catch a redhead (*Aythya americana*), a northern pintail (*Anas acuta*), a Forster's tern (*Sterna forsteri*), and a laughing gull (*Larus atricilla*). An adult female chased a northern harrier, pirating the rodent it carried.

DISCUSSION

The Laguna Madre and associated tidal flats on the east and west side create a vast, shallow, foraging habitat for uncountable numbers of wading birds and waterfowl. Over 35 000 redheads alone winter there (S. Thompson pers. comm.). Only the dunes on SPI and the low headlands on the mainland are not subject to frequent inundation. The margins of the laguna shift over several kilometers, resulting in a rich but featureless landscape devoid of places for prey to escape hunting peregrines. C. Thelander and P. Bloom (in Hunt and Ward 1988) found peregrines wintering in barren habitat in coastal Peru similar to SPI.

The majority of the positions of peregrines we determined were on tidal flats or adjacent perches on the Laguna Madre. Seldom did the falcons perch near the gulf beaches or fly inland to agricultural land. In the same area, Hunt and Ward (1988) located 24 radio-tagged peregrines on tidal flats about 67% of the time in the April 1979 and 1980 migration period.

Our observations of attacks on prey suggest hunting is often on the tidal flats, especially near the laguna. Perches on the laguna provided resting places for peregrines. This is unlike the many observations on the Culiacán Marsh in Sinaloa where most kills were over water and prey was limited to ducks and other birds small enough to be carried (Enderson et al. 1991).

In 1993, first-year peregrines seemed to move in different patterns (Fig. 1) compared to 1994 (Fig. 2). This may be a sampling artifact. In 1993, we usually sought to locate each bird visually, guided by telemetry; locations therefore included fewer inaccessible sites on the laguna. In 1994, locations produced mainly by triangulation were not limited in that way. However, maximum dispersion of first-year birds in both years was similar.

We saw about 20 individual peregrines in the Laguna Madre area south of Mansfield Channel in 1994. More were undoubtedly present but population estimation is risky. The extent of vast tidal flats is limited on the coast of the western Gulf of Mexico. Flats extend northward only 140 km from the town of South Padre Island. Based on our observations at the southern end, that region of tidal flats may have had 60 or more peregrines in 1994. There are vast flats southward 90 km in Mexico. Elsewhere along the gulf coast, peregrines may over-winter in other habitats. The Florida Game and Fresh Water Fish

Commission recently estimated 200–300 arctic peregrines winter in the state (USFWS 1994).

Coastal Texas and adjacent Mexico, and the Maryland and Virginia coasts are the two major migration focal points of arctic peregrines (Yates et al. 1988). Kiff (1988) estimated the number of historical pairs of these northern peregrines at between 5000 and 8000; recently, Peakall (1990) considered the health of that population to be good. These migrants, including the greatly under-represented adult male component, move rapidly southward at SPI (Chavez-Ramirez et al. 1994) but some remain in winter. In April, northbound migrants stage at SPI prior to return to the Arctic, no doubt attracted by easy hunting. About 16% of 170 peregrines seen in spring on SPI in 1994 were retaining much of their first-year plumages, indicating some of these birds, about to become yearlings, move northward in their first spring (T. Maechtle and W. Seegar pers. comm.). Cade (1960) did not see yearling peregrines in arctic Alaska and we speculate some of these young birds may remain in summer, like Ospreys (Henny and Wight 1969), in the winter habitat of adults on the Laguna Madre.

The emerging picture is one of hundreds, perhaps thousands, of peregrines wintering on the southern coasts of North America each year. The present study suggests these birds may not be continually traveling. If peregrines elsewhere in winter show the degree of aggression toward conspecifics we saw, further study might confirm that adults, at least, are territorial in winter.

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FALL CONCENTRATIONS OF BUTEOS NEAR THE CONTINENTAL DIVIDE: A TWENTY-YEAR SUMMARY

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ABSTRACT.—Since 1974, we have counted raptors at Henry's Lake, Idaho, just south of the continental divide. Counts were made in late summer and early fall. Three species, red-tailed hawk (*Buteo jamaicensis*), ferruginous hawk (*Buteo regalis*), and Swainson's hawks (*Buteo swainsoni*) were the most plentiful. None of these hawks showed any strong increasing or decreasing trend in numbers over the 20-yr survey period, but all three showed a large increase in numbers subsequent to the end of a drought in 1977. We suggest that in some cases, a small number of counts may provide useful data, and that counts in different locations might provide information on migratory strategies of adults and juveniles.

KEY WORDS: *Buteo jamaicensis*; *Buteo regalis*; *Buteo swainsoni*; *ferruginous hawk*; *migration*; *red-tailed hawk*; *Swainson's hawk*.

Concentraciones de *Buteos* en otoño cerca de la división continental: un resumen de veinte 20 años

RESUMEN.—Desde 1974 hemos contado rapaces en Henry's Lake, Idaho, al sur de la división continental. Los conteos fueron hechos hacia el final de verano y a principios de otoño. Tres especies, *Buteo jamaicensis*, *Buteo regalis* y *Buteo swainsoni* fueron las más abundantes. Ninguno de estos aguiluchos mostraron tendencias a incrementar o disminuir sus números en un período de 20 años de estudio, pero las tres especies de *Buteo* mostraron un gran incremento en sus números posteriorm a una sequía en 1977. Sugerimos que en algunos casos, un pequeño número de conteos puede proveer útiles datos y conteos en diferentes localidades pueden proveer de información sobre estrategias migratorias de adultos y juveniles.

[Traducción de Ivan Lazo]

Starting in 1974, we (Trost and others) counted raptors, primarily buteos, every year during their fall migration at Henry's Lake, Idaho. Results to 1983 were reported previously (Taylor and Trost 1985). We used road counts for these surveys, rather than the stationary counts usually employed for migration counts (Fuller and Mosher 1987). More recently, we have expanded the number of counts made each fall. Our purpose was to evaluate the importance of these extensive meadows near the continental divide as a short-term foraging site, and to characterize the timing and duration of hawk migration in the area. Under the conditions of our survey, we found that a limited number of road counts yields useful information on migrating raptors.

METHODS

Henry's Lake is located in northeastern Idaho, near the border with Montana west of Yellowstone National Park. The area surrounding the lake is largely wet meadows and big sagebrush (*Artemisia tridentata*) flats; elevation of these areas is about 2000 m. Much of the area is used for cattle grazing; some of the grazed area is sagebrush grass-

land and a small portion is irrigated pasture. The flats around the lake represent the majority of the treeless area in the vicinity. Stands of conifers surround the basin with lodgepole pine (*Pinus contorta*) on the lower slopes and Douglas fir (*Pseudotsuga menziesii*) more plentiful on the mountain slopes to the west and south. Henry's Lake lies at the north end of a north to south valley through which the Henry's Fork of the Snake River flows south to the Snake River Plain above the town of Ashton, Idaho. The Centennial Mountains are to the west and the Henry's Lake Mountains lie to the east. North of the lake, Reynolds Pass leads to the broad valley of the Madison River, which opens into the plains of southwestern Montana. Thus, the Henry's Lake area may be in a natural migratory corridor between the northern plains and the Snake River plain. In this respect, the study area may be like traditional hawk-watch sites, which are usually located where geographic factors concentrate hawks into a small area.

Our survey route covered approximately 53 km around the lake, primarily through open areas but extending into patchy lodgepole pine habitat on the south side of the lake for approximately 6 km. We surveyed between the middle of August and the end of September. Surveys started at approximately 0630 H, and we attempted to finish before 1030 H. We counted all raptors seen along the survey route. Since most of the terrain is open, some were counted

at distances up to 400 m or more, but most were counted on power poles or fence lines within 100 m of the road. During this time of day raptors generally remained perched, either in trees or on the numerous power poles and fence lines in the vicinity. Mornings were cold during the survey period, and warmed slowly to temperatures appropriate for soaring by hawks. We seldom saw raptors flying or soaring until the very end of a day's count, indicating that we were unlikely to double-count birds. For more detail on the survey method, see Taylor and Trost (1985).

We present our summary of the number of hawks observed each year as either a single survey in a given year (1974–79, 1981, 1984, 1986, 1987), the average of two observations (1980, 1982, 1983, 1985), or the average of three or more counts (all other years). Thus, the numbers differ slightly from those previously reported, because Taylor and Trost (1985) used the high count from each year with two counts (none of the years they reported had more than two counts). For 1990 through 1993, the number of hawks is the average of counts made between 18 August and 14 September, although we made counts before and after these dates. Counts in earlier years were made between these dates, so the timing of observations is consistent for all years. In addition, numbers of hawks counted tended to decline after 14 September (see below). Thus, all counts were made near the time when hawk numbers peak in the study area.

RESULTS AND DISCUSSION

The most frequently observed raptors were the red-tailed hawk (*Buteo jamaicensis*), Swainson's hawk (*Buteo swainsoni*), and ferruginous hawk (*Buteo regalis*). We report only the data for these three species.

Our counts show no clear increase or decrease in the numbers of these three species from 1974–93 (Fig. 1). However, all three hawks increased substantially in numbers from 1979–81, with subsequent counts falling to approximately pre-1979 levels.

Swainson's hawks are sometimes considered to be declining, either in the West as a whole (White 1994) or regionally (Harlow and Bloom 1989), but our counts showed relatively steady numbers of this species. Many observers (cited in Olendorff 1993) have considered ferruginous hawks to be declining in numbers. Figure 1 shows no strong trend in counts of this species, although there may be a slight downward trend overall.

Ferruginous hawks observed at Henry's Lake may be following the continental divide from north to south, since they often migrate in a north to south direction along the divide (Harmata 1981). They may also be reacting to prey availability by migrating eastward up the Snake River plain. At lower elevations near Boise, ground squirrels (*Spermophilus* spp.) begin estivation in early July, and black-tailed

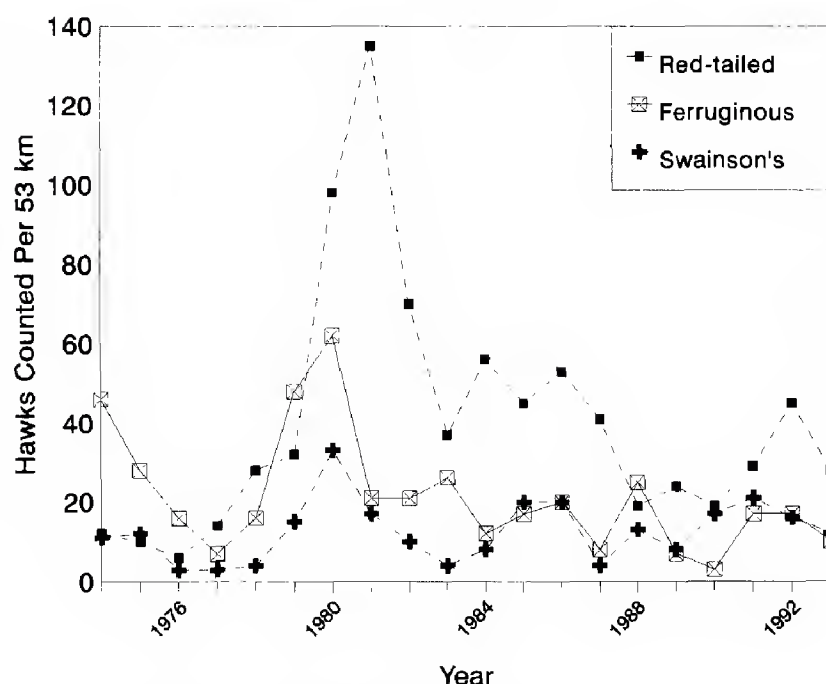


Figure 1. Counts of red-tailed, ferruginous, and Swainson's hawks near Henry's Lake, Idaho, from 1974–93. Numbers are the averages of counts taken between 18 August and 14 September (some years include only a single count; see text).

jackrabbits (*Lepus californicus*) become inactive during the day. The hawks then move eastward through the Henry's Lake area and other montane meadows, where ground squirrels remain active until late August. They may then move across the divide and into the Yellowstone National Park area (Thurrow et al. 1980). Thus, our counts may reflect hawks moving both from the north and from the southeast. In addition, our data may include some juveniles fledged from relatively local nesting areas.

Peak hawk migration at Henry's Lake occurred in late August and early September (Fig. 2). Counts within a given year show the same fairly smooth pattern as the weekly averages shown in Fig. 2, with peak numbers in the last week of August or the first week of September. This indicates that our observations prior to 1990 most probably occurred near the peak of migration, and we feel that Fig. 1 gives a good representation of migratory hawk numbers at Henry's Lake.

The sharp increase in overall numbers in 1980–81 (Fig. 1) is thus likely to be real and not an artifact of the small number of counts in earlier years. The limited number of data points precludes statistical analysis, but the coincidence both in peak years and in the shape of the curve for all three species, as well as the fact that numbers of red-tailed and ferruginous hawks were substantially higher than those observed

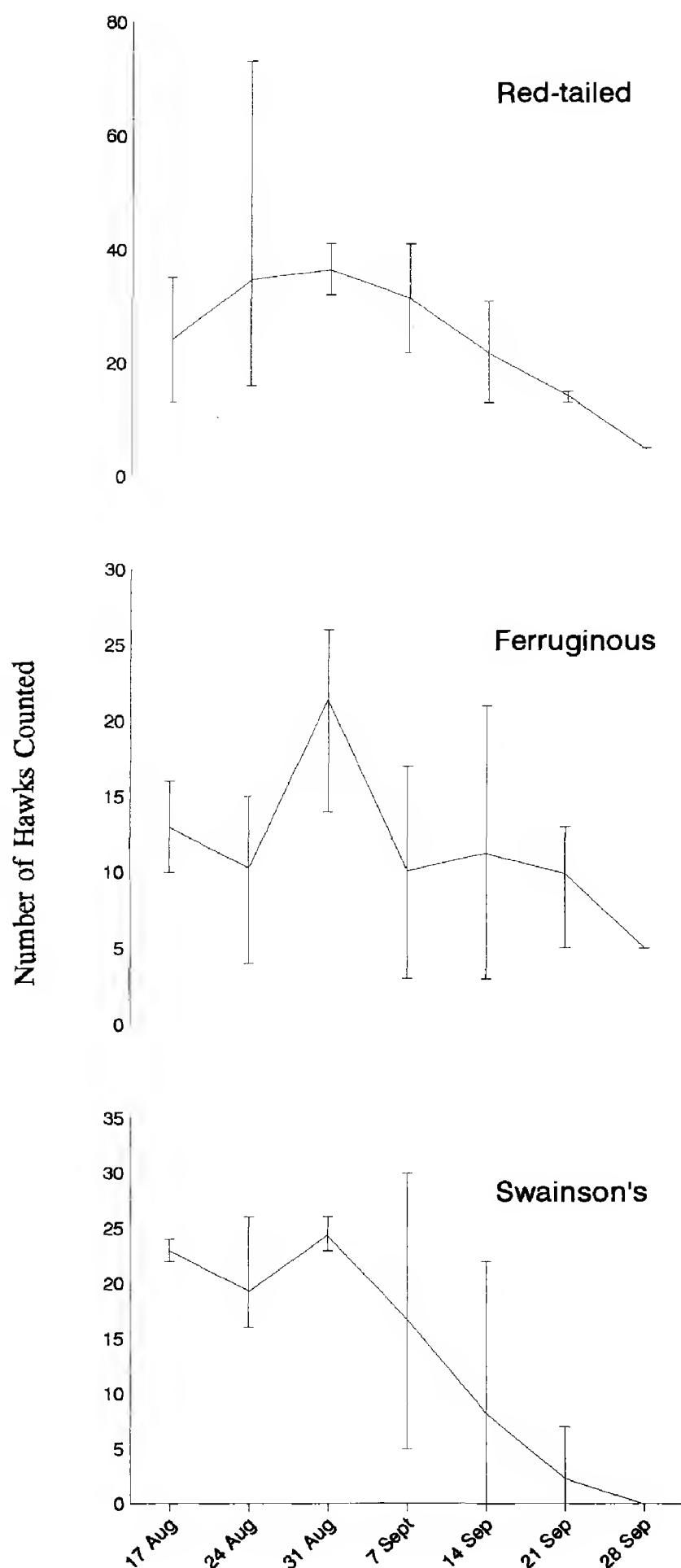


Figure 2. Counts of red-tailed, ferruginous, and Swainson's hawks near Henry's Lake, Idaho, from early August to late September, 1990-93. Vertical bars show maximum and minimum numbers observed in these years; average numbers for the four years are connected by the straight lines. Counts were made in the week preceding the date

in other years, gives confidence to the conclusion that hawk numbers were exceptionally high in these years.

These high counts might be due to advantageous local conditions that attracted an unusual number of migrating buteos. However, the counts could also reflect population increases after the prolonged drought of 1973-77, which occurred over most of western North America. A recovery in hawk populations subsequent to a drought might be delayed until after prey populations recover, accounting for the rise in counts in 1980-81 rather than immediately after the end of the drought. We are continuing the surveys, and will be able to determine if any similar pattern occurs following the end of the current drought (which continues despite high precipitation in winter 1992-93).

Hawk counts from our surveys may yield somewhat different results than those obtained at traditional hawk-watch sites. At those sites, hawks are channeled through a very small area by geographic factors, and the hawks counted are presumably a representative sample of all age classes and both sexes in the population. Local surveys, in contrast, may count a nonrepresentative sample of the population, since adult and immature hawks do not generally migrate together (Newton 1979).

Some of the hawks we observed might have been juveniles moving from their natal areas prior to actual southward migratory movement. Our peak numbers for red-tailed and ferruginous hawks occur earlier than other observed migration times in the northern United States, which show red-tailed hawks dispersing in August and moving southward in mid-September and ferruginous hawks starting migration in late September, after ground squirrels begin hibernation (Palmer 1988). However, the position of Henry's Lake south of the western Montana plains and between two mountain ranges indicates its potential as a stopover point on a migratory corridor, and our early dates may simply be the result of the northern latitude of the study site. Since the Henry's Lake area offers limited nesting habitat for Swainson's and ferruginous hawks, the appearance of a large number of juveniles prior to actual migration could indicate that their post-fledging movements are not random in direction.

←

shown; only one count was made for the week of 28 September.

Hawk counts require a considerable expenditure of time and money. Based on our data, we suggest that in areas where migration peaks at a consistent time of year, a relatively small number of counts may result in very useful data. Counts in areas of varying habitat and topography could be used to investigate differences in migratory habitat use by adults and immatures, as well as general habitat use during post-fledging movement and migration. Identification of this habitat may be of considerable importance for raptor conservation: the area surrounding Henry's Lake has been subdivided and the number of houses is increasing rapidly. If this and other similar areas are important migratory staging or stopover areas, they should be identified and protected.

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MODIFICATION OF PARENTAL BEHAVIOR DURING THE NESTING PERIOD IN THE COMMON BUZZARD (*Buteo buteo*)

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ABSTRACT.—The nesting behavior at five nests of common buzzards (*Buteo buteo*) was studied—two by video camera and three by direct observation. The objectives were to describe female behavior and to determine the proximate causes explaining why the female spent less time at the nest as the chicks grew. Before hatching, the female incubated almost constantly. The second period (days 0–8 after hatching) involved an active brooding pattern that occurred during feeding sessions. The third period (days 9–30) was characterized by a decrease in the variety of behavior performed by the female. Except for delivering prey, males were rarely involved in the direct care of the young. Furthermore, females did not deliver prey to the nest once they began to leave the young unbrooded for increasing periods of time. The female provided essentially all the care to the young after hatching. Her parental behavior was thwarted later by the increasing activity of the growing young, which is shown by a strong correlation between the time spent by the female at the nest and the activity of the young. This activity apparently led to the female's reluctance to stay at the nest in the presence of active young.

KEY WORDS: *behavior; Buteo buteo; incubation period; nestling period; parental care; prey delivery; reproduction.*

Cambio en la conducta parental durante el período de nidificación de *Buteo buteo*

RESUMEN.—Estudiamos la conducta de nidificación de *Buteo buteo* a través de registros de video y observaciones directas. Describimos la conducta de nidificación de la hembra y determinamos las causas proximas que podrían explicar la disminución progresiva del gasto en tiempo tanto en el nido como en la crianza de los pollos. Inicialmente, la hembra incubó casi constantemente. El segundo período (0–8 días después de la eclosión) involucró un activo patrón de ampolamiento que ocurrió durante las sesiones de alimentarias. El tercer período (9–30 días) se caracterizó por una disminución en la variedad de conductas desempeñadas por la hembra. Las hembras no entregaron presas en el nido hasta que comenzaron a dejar los juveniles por mayores períodos de tiempo. La hembra proveyó de todos los cuidados necesarios a los juveniles luego de la eclosión, pero más tarde, su conducta parental fue impedida por el aumento de actividad de los juveniles, lo que mostró una fuerte correlación entre la disminución del gasto de tiempo de las hembras en el nido y la actividad de los juveniles. Excepto por la provisión de presas, los machos, raramente se involucraron en el cuidado directo de los juveniles.

In most raptorial species the nest is attended by adults from 90–100% of the day during incubation and the first days after hatching (Rowe 1947, Rettig 1978, Stinson et al. 1988). In some species, the female becomes reluctant to leave the nest shortly before hatching, even at the approach of the male with food (Newton 1979). In those species in which males contribute to incubation, the female, usually dominant over the male (Carlier and Gallo 1989, Hubert and Carlier 1992), does not allow the male to perform incubation during the days immediately pre-

ceding and following hatching (Liversidge 1962, Wiley and Wiley 1981, Dewhurst et al. 1988, Village 1990).

Brooding behavior seems to wane after the nestlings have attained their second down plumage, as suggested in the gyrfalcon (*Falco rusticolus*; Jenkins 1978), or after becoming able to control their own body temperature, as suggested in the Eurasian kestrel (*Falco tinnunculus*; Village 1990). Once the female stops brooding, she spends most of her time in the vicinity of the nest (Wiley and Wiley 1981).

Nest attendance progressively reduces to feeding bouts and finally to food deliveries to the young. In most raptors, the transition between these phases is gradual and can occur on different schedules from nest to nest within the same species (Newton 1979). Although this nest attendance pattern has been described in several species, data are lacking for the common buzzard (*Buteo buteo*; Hubert 1990).

Most studies of the parental behavior in raptors implicitly assume that the adults behave in a way to satisfy the nestlings' needs (Jenkins 1978, Village 1990). For instance, adult hawks assist the thermoregulation of their nestlings by brooding or shading when chicks are small (Newton 1979), whereas the subsequent waning of female nest attendance is usually linked with the increasing nutritional needs of the young. In many species studied, the females do not deliver prey to the nest once they begin to leave the young unbrooded (Matray 1974, Jenkins 1978, Wiley and Wiley 1981). In the Eurasian kestrel, some females were never observed bringing prey to the nest during the nestling stage and attended the nest only during the first week following hatching (Village 1990). Why do females then leave the nest if not for hunting? Could other reasons explain the gradual waning of time spent by females at their nests?

Although natural selection would favor behavior that enhances nestling survival, the proximate factors motivating a bird to perform a particular behavior may be completely different from the evolutionary function. What are the proximate causes of the modification of the parental behavior? The aim of the paper is to test if buzzard females (1) leave the nest to satisfy the increasing nutritional needs of the young, or (2) leave the nest for another reason. One possible alternate explanation is that females leave the nest because of the increasing activity of the young, leading to an increasing avoidance of the young by the female.

METHODS

Area and Nest Sites. Nest-site characteristics have been described previously (Hubert 1992, 1993). We observed five pairs of buzzards nesting in the forest of Chizé (Deux-Sèvres, France) which is mainly composed of beech (*Fagus sylvatica*), oak (*Quercus pedunculata*) and pine (*Pinus sylvestris*). Nest trees were either beech, oak, or pine, and were located near pathways to facilitate a quiet and rapid approach by investigators. Nests were at a height of 14–20 m. Two nests were monitored by video camera and three by direct observation. Observations were made from 2 May to 10 June 1991.

Direct Observation. Three nests (nests C, D, and E) were monitored from ground level with a telescope (20–60×) and binoculars (8×) from observation sites 20–40 m from the nests for a total of 168 hr. The three nests were observed in succession in the morning for about 6 hr each per day. Nest C, containing one young, was observed directly from days 4–24 after hatching, then by video camera from days 28–45. Nest D, containing three young, was observed 5 d before to 10 d after hatching at which time the whole clutch suffered depredation. Nest E, containing three young at the beginning was observed from days 11–34 after hatching, but two young were killed by siblings (at age 14 and 32 d respectively) and the last one was found dead under the nest at age 37 d.

Video-recorded Nests. A video system, composed of a camera and a portable recorder powered by an automobile battery, was placed at two nests (A and B) each containing two eggs. The cameras (each protected by a plexiglas and wooden box and camouflaged by tree branches) were installed in trees 3–4 m above and 8–12 m from the nests. Each morning, at a fixed solar time, a new 4-hr tape was placed in the recorder. This created a small disturbance at the nest: the incubating female took off and returned 2–3 min later. This sampling regime was chosen because it appeared to be the time of maximum nesting activity in a preliminary study of full-day nest activity (Hubert 1990). Recording was done from 5 d before hatching until 18 d after hatching for nest A. The second young of nest A was killed by a predator in its 18th day of life (the first one died by sibling competition at 4 d). Then the video system was moved to nest C. Nest B was recorded from 13 d before to 32 d after hatching. Only one egg hatched, and this young was monitored until it was 32 d old. A total of 324 hr were filmed at the three nests (A, B, and C). Only the young of nest C was observed until flight, 43 days after hatching.

Behavioral Analyses. Video tapes were examined using a detailed ethogram describing movements, postures adopted, and the location of the behavior in the nest. The ethogram included 127 behaviors, but only the 34 acts occurring in behavioral sequences and appearing in correspondence analyses are described (Table 1). Videos were analyzed once by the same worker (C.H.), usually at normal speed, but some sequences (e.g., feeding bouts, nest arrivals, relationships between mates) were watched several times and slow motion was used. Data from direct observation nests were mainly used to ensure that recorded nests were consistent with other nests, but could not be as detailed as data from recorded nests.

Statistical Analyses. Behavioral sequences were statistically analyzed with SPAD.T software (described in Lebart et al. 1984, Morineau 1984, Lebart and Salem 1988), which can process a large number of diversified lexical data. Multifactorial data analyses were applied to the behavior of the females recorded at nests A and B (nest C was recorded too late in the nesting period to collect a large amount of data concerning the behavior of the female). Describing the behavior as a succession of acts (e.g., A, B, C, D, B, A, B) results in arbitrary breaks in a continuous activity. In order to regenerate natural groups of behavioral events with their transitions, series of repeated sequences of events were first identified (A–B, B–

Table 1. Non-exhaustive ethogram of female common buzzards at the nest. Only the acts involved in specific chains of behavioral sequences appearing on correspondence analyses are listed here (see methods).

AAC:	alarm attitude performed in the nest cup
AAR:	alarm attitude performed on the nest rim
ABR:	basic attitude of female landing at the nest (slanted, head in the neck, tail more or less spread)
AFC:	flattening in the nest cup while sitting on eggs
ASC:	scanning attitudes performed sitting in the nest cup
ASR:	scanning attitudes performed on the nest rim
ASS:	scanning attitudes performed standing up in the cup
BRC:	moving branches belonging to the rim from the center
F2:	tearing the prey into morsels
F3:	giving a food morsel to the young
F5:	morsel refused by young
F6:	ingesting morsel
F7:	picking up a fallen morsel
GUC:	getting completely up from the nest cup
GBC:	getting up backing off from the nest cup
GHC:	getting half up from the nest cup
H2C:	a series of two calls from the nest cup
H3C:	a series of three calls from the nest cup
INC:	incubation, sitting still on the eggs or young
PNC:	preening of the neck in the nest cup
PSC:	head-shake in the nest cup
PWC:	preening of the wing in the nest cup
ROC:	rocking movements (in order to place the clutch well in contact with her brood patch) while settling down or already sitting in the cup
RCC:	looking at the center (eggs or young) from the nest cup
RRC:	looking at the center (eggs or young) from the nest rim
SDC:	stepping down into the nest cup
THC:	turning herself in the nest cup
TEC:	this act refers to two different action patterns, the first one described by Gargett (1990) results in eggs turning: the female stretches her head forward and down to place her beak tip in front of the egg, slowly moving the egg toward her until it disappears beneath her breast feathers. The second one described by Ellis (1979) as 'bill-dig,' is a behavior oriented to the nest, where the beak and cere are buried in the nest cup. These actions were not always distinguishable and were combined as the same act, TEC.
WRR:	walking on the nest rim.

C, C-D, D-B, B-A, A-B-C, B-C-D, etc.). A threshold was applied to eliminate rare sequences and to retain the 150 more frequent sequences. Frequency tables were computed with the repeated sequences (A-B, B-C, C-D . . .) in lines and in rows for the observation days. The statistical association between lines and rows was then established (by calculations of the chi-square distance) and represented graphically by a correspondence analysis. Thus, a correspondence analysis illustrates the statistical relationships between sequences of acts and observation days, represented by a cluster of points. In two-dimensional space, the F1 factor is the main axis explaining most of the total variance. The F2 axis is the second most important factor in explaining the total variance, orthogonal to F1. On the graph, days with similar behavioral profiles are positioned closer. On the contrary, if days or sequences of acts are represented far away on one factor, it emphasizes an opposition between these days or these behavioral sequences for the concerned factor. Furthermore, evolution of female behavior from day to day is well described and characterized by the specific chains.

The most characteristic sequences ($N = 15$) were listed for each factor of the analysis. Rather than representing them on the graphs, transitions in groups of events were regenerated; e.g., the sequences A-B-C, C-B, and C-D were represented by the chain $A \rightarrow B \leftrightarrow C \rightarrow D$. Only the chains with the highest contribution to factors ($N = 15$) are represented in the figures.

Means are given with standard deviations. A Bravais-Pearson correlation test was used to calculate the link between the time spent by the female at the nest and the time during which the young was active (expressed in percent of observation time). The time of activity of the young was measured by the total sum of time spent in activities other than sleeping or being brooded.

RESULTS

Nest Attendance Schedule of Males and Females. Nest attendance of the females generally decreased 5–10 d after hatching (Fig. 1). The male, when allowed access to the nests (nests B and D), showed no regular pattern of attendance throughout the incubation period (maximum male attendance length observed was 1 hr, mean duration of stay during the incubation period was 6.5 min (SD = 3.6) at nest B and 3.0 min (SD = 1.0) at nest D, where males performed incubation). From 11–15 d after hatching, the females spent less than 50% of the observation time at the nest. About 25 d after hatching, females spent as little time at most nests as did males (except nest B).

After 15 d, the female of nest B was present at the nest more than the other females. Her nestling seemed slightly retarded compared to the average (at 31 d, it was still unable to eat alone and its feathers were less well developed than in other young of the same age). Because the young of nest A did not show

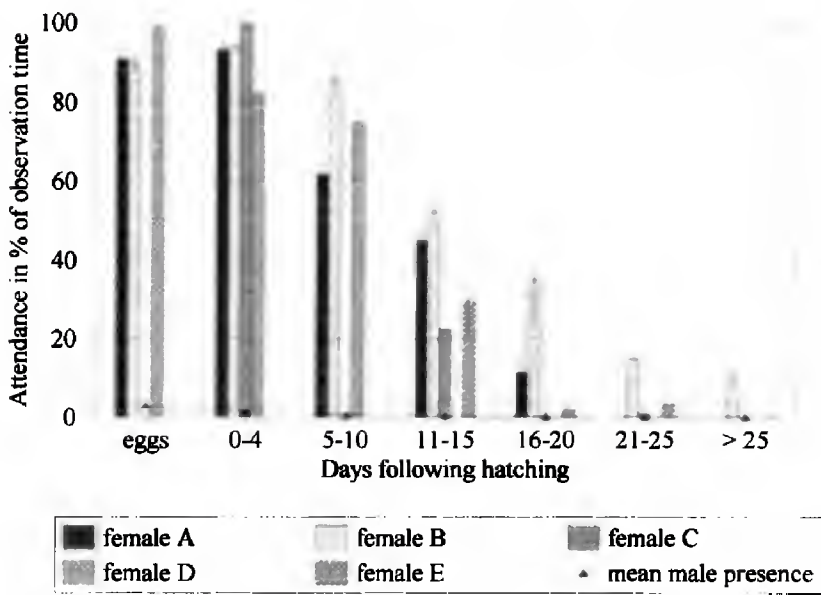


Figure 1. Common buzzard nest attendance in the forest of Chizé (France), observed from 2 May to 10 June 1991 (vertical lines are standard deviations).

an identical delayed growing pattern, this may not be due to an effect of the camera, but rather to different growing pattern between young.

Number of Prey Delivered by the Females According to the Age of the Young. The videotaped females (nests A and B) started to deliver some prey after the young were 16 d old (Fig. 2). But, their contribution in prey deliveries was equal to that of their mate at 25 or more days after hatching. Although females attended the nest for less than 50% of the observation time after 10 d, they did not deliver a substantial amount of prey until about 20 d. The number of prey delivered by adults at nests directly observed (nests C, D, and E) could not be estimated because the prey was usually not identifiable unless it was carried in the beak.

Analysis of the Behavior of the Female at Nest A. Correspondence analysis (Fig. 3) points out the relative similarity of days from (E-5)-Y8, opposed to days Y9-Y18 on the axis F1. There was no strong change in the behavioral profile of the female between 5 d before hatching and 8 d after. The behavior of the female incubating eggs or brooding a chick a few days old was about the same. From 5 d before to 8 d after hatching (Fig. 3), incubation/brooding (INC) was the primary behavioral activity, but a great number of acts were also involved. Chains of acts were long and involved a great diversity of acts. In Fig. 3, groups (E-1)-(E-5) and Y2-Y8 are distant on the second axis due to the emergence of feeding sessions.

The change in the female behavior occurred at 8-9 d after hatching. From Y9 to Y18, the female

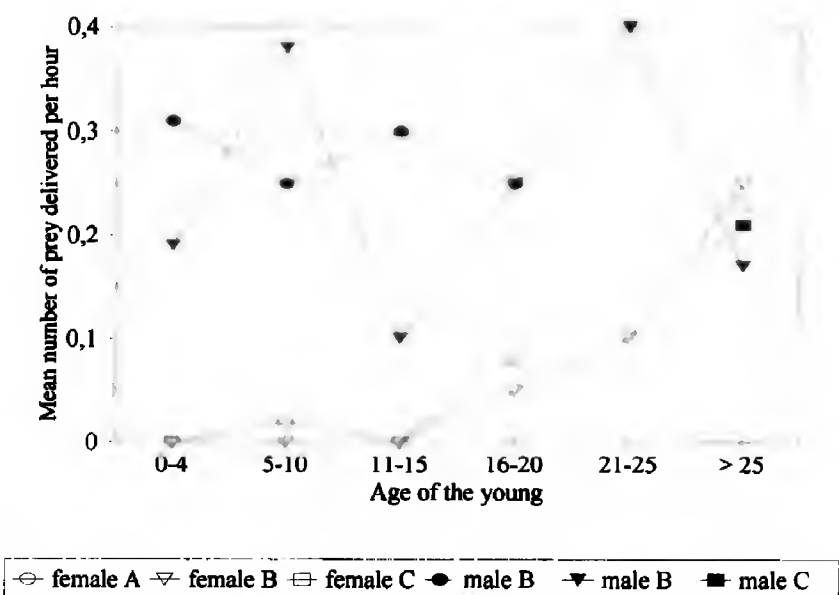


Figure 2. Number of prey items delivered to nest per hour by male and female common buzzards according to the age of the young (Forest of Chizé, 2 May to 10 June 1991).

behaved in a very homogeneous style (proximity of the points, Fig. 3). These days were typified by more effective feeding sessions. During Y9-Y18, females gave most of the food morsels to the young, whereas during Y2-Y8 the female ingested most of the torn morsels. Chains of acts were short and did not involve a great number of acts.

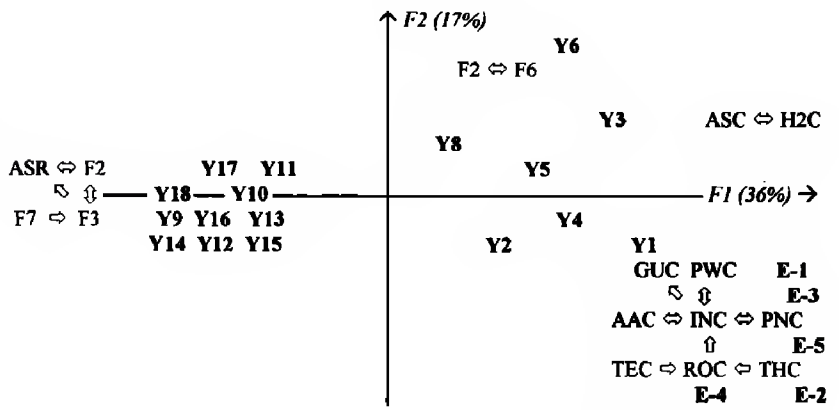


Figure 3. Correspondence analysis of the behavior of the female common buzzard at nest A according to the different observation days. See text for the explanation of chain construction and Table 1 for description of acts. Days (in bold characters) indicated the time preceding or following hatching; e.g., E-3 means 3 d before hatching (E = eggs), Y3 means 3 d after hatching (Y = young). Note the opposition on axis F1 between days (E-5)-Y8 and days Y9-Y18. The change in the female behavior occurred at 8-9 d after hatching. The group of days (E-5)-Y8 was characterized by incubation/brooding involving a great diversity of acts. The group of days Y9-Y17 was characterized by a reduction in the diversity of acts performed by the female (behavior reduced to feeding sequences).

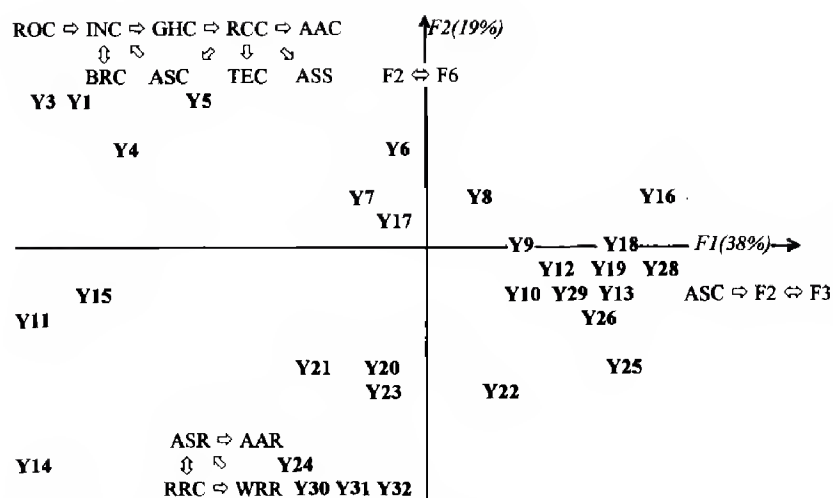


Figure 4. Correspondence analysis of the behavior of the female common buzzard at nest B after hatching. Acts belonging to a chain are described in Table 1. Days (in bold) indicated the time following hatching; e.g., Y6 means 6 d after hatching. Note the separation on axis F1 of days Y11, Y14, Y15 (days without feeding sessions at a stage where feeding occurred intensively), and separation of days Y1–Y8 from days Y9–Y32 (except Y16 and Y17, rainy days) on axis F2. Evolution of the female behavior occurred between the first days after hatching (characterized by a great diversity of acts), days Y9–Y25 (characterized by intense feeding sequences), and days Y30–Y32 (characterized by alarm attitudes on the nest rim).

Analysis of the Behavior of the Female at Nest B. Days Y1–Y8 were characterized by brooding behavior (Fig. 4), where the female performed a great number of diversified acts. Chains of behavioral acts were long and involved a great diversity of acts. Y16 and Y17 are included in this group because these

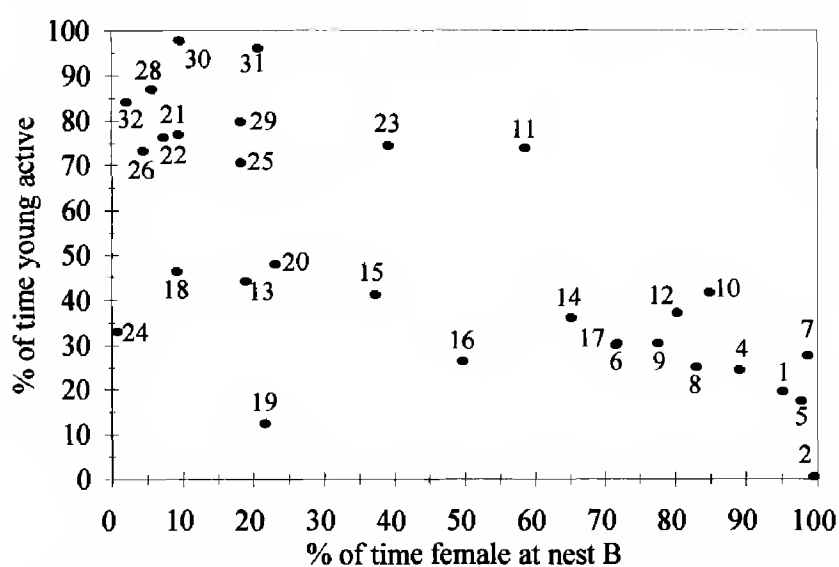


Figure 5. Correlation between time spent by the female common buzzard at the nest and the time of activity of the young (total of the time spent in activities other than sleeping or being brooded) recorded during 4-hr per day at the nest B ($r = -0.71$, $A = -0.92$, $N = 30$, $P < 0.01\%$). Numbers correspond to the age of the young.

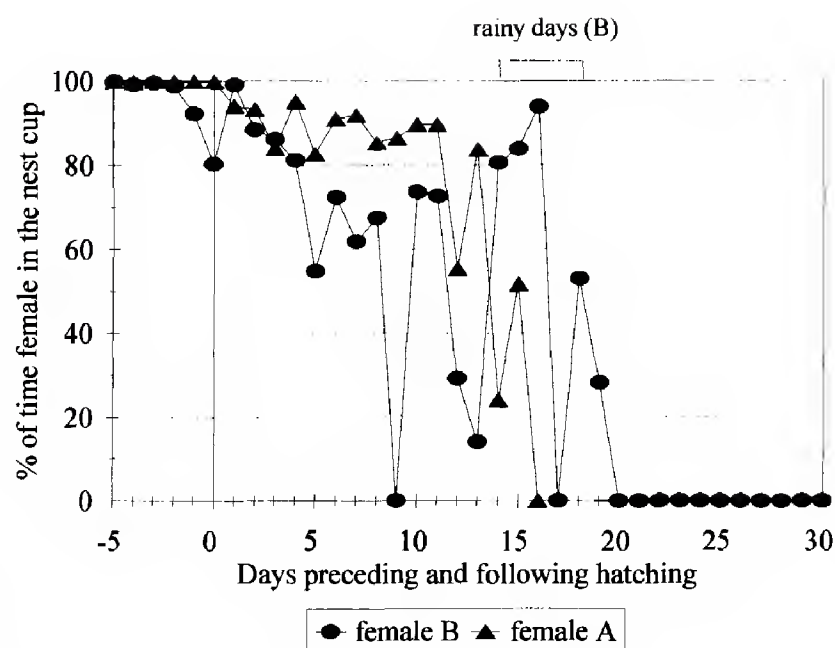


Figure 6. Time spent by female common buzzards in the nest cup versus the age of the young.

days were rainy (Y19 and Y20 also), and on both days the female behaved much the same as in the brooding period: she reached the nest as soon as it started to rain and stood over the young in the nest cup. Because of this behavior, these days are similar to days when the young were very small.

Y9–Y19 showed a decrease in the number and in the diversity of acts performed by the female at the nest (except during rainy days, Y16 and Y17) and intense feeding sessions (with F2–F3). The points are well clumped showing the homogeneity of the behavioral profiles on these days, if the young were fed (days Y11, Y14, and Y15 are widely separated from any group of points because these days were without feeding sessions at a stage where feeding occurred intensively).

As the young grew older, the female engaged more and more in many alarm and scanning attitudes (AAR, ASR), glances toward the nestling (RRC), and walking on the rim (WRR). During this period time at the nest was reduced to feeding sessions.

Observations at nests C and E revealed that after 30 d following hatching, the female, like the male, landed at the nest only to deliver prey. Her stays were reduced to a few seconds, the nestlings being able to eat alone. At this stage, the young begged aggressively to the arriving bird. Furthermore, the female did not exhibit her basic attitude (ABR) when landing at the nest, but exhibited the same alarm posture (AAR) as the arriving male.

Correlation Between the Time Spent by the Female at the Nest and the Time of Activity of

the Young for Nest B. The strong correlation (Fig. 5, $r = 0.71$, $r^2 = 0.5$, $P < 0.01\%$, $N = 30$) indicated that the activity of the young explained very largely the pattern of the female nest attendance. The more the young were active, the less the female was present at the nest. Note that the days are not well arranged in chronological order (Fig. 5).

Time Spent by Females A and B in the Nest Cup According to the Age of the Young. We observed that females attended the young until the nestlings were about 20 d old (Fig. 1). But the time spent by females A and B in the nest cup decreased after about 12 d (Fig. 6), whereas the time spent on the nest rim (and away from the nest) increased. After 15 d (except during rainy days in nest B where the female stood up in the nest cup), neither of the females ever entered the nest cup, and their stays at the nest were restricted to the nest rim.

DISCUSSION

Our results showed that as the young became older the variety of behavior performed by females at the nest was more and more limited. Furthermore, the area of the nest they occupied frequently was increasingly restricted. Thus, the performance of diversified behavior of females could be prevented by the presence of more and more active young in the nest. Furthermore, the fact that female nest attendance pattern was strongly correlated with the activity pattern of the young suggests that the female seemed to increasingly avoid contact with the active young. This avoidance behavior of the female seems to appear progressively (according to the correspondence analyses), but it is much more evident at a later stage of the nesting period. Indeed, after 25–30 d females behaved in the same way as males when landing at the nest. At this stage, not only the activity of the young increased, but the young were physically and behaviorally very different. Only the nestlings' head and neck were covered with down and the young adopted begging postures and mantled (wings and tail spread) over the prey.

Furthermore, this adult "avoidance hypothesis" seems to be consistent with findings of other authors. A reluctance of the adults to remain near their fledged young was noticed in some raptorial species (Jenkins 1978, Alonso et al. 1987, Gargett 1990). Nearly fledged golden eagles (*Aquila chrysaetos*) were even observed attacking their parents (Ellis 1979). In the black kite (*Milvus migrans*), before the first flights of the young, there was an increase in the amount

of time adults spent flying with prey in their talons before entering the nest (Bustamante and Hiraldo 1990). This could mean that the parent is reluctant to enter the nest with the aggressively begging young. Even though the literature shows that females have difficulty getting into the nest cup if it is full of large, aggressively begging young, our results show that females decreased brooding behavior before the size of the young for brooding became a factor (ca. 11–15 d). In the buzzard, it appears that the activity level of the young repels the parents rather than the performance of a particular behavior (such as begging). The "avoidance hypothesis" is consistent with the fact that the females did not leave the nest to hunt, because they did not deliver a substantial amount of prey before the young were over 25 days old.

During rainy days, the female was able to perform brooding: she landed at the nest and the 15–20-d-old young did not beg for food. She could stay in the nest cup with the young lying quietly under her until the rain ended. In other species, half-grown nestlings were also observed to be brooded during heavy rains or during windchills even though brooding in general had come to an end (Newton 1978, Jenkins 1978, Ellis 1979). Even if the ultimate explanation for this behavior is linked with the enhanced survival of offspring brooded during rain, the proximate cue for brooding in poor weather could be that the chicks, inactivity stimulates brooding. This hypothesis needs to be tested experimentally.

Our data suggest that the behavior of the female at the nest seems to be a compromise between her own motivation, environmental factors, and the behavior of the young. The brooding pattern of the female buzzard is freely performed until 9 d after hatching. Thereafter, the activity pattern of the female is characterized by a decreasing variety of acts on a decreasing area of the nest which is linked to the increasing activity of the young, and probably leading to the reluctance of the female to stay at the nest. Our conclusions cannot completely eliminate the possibility that the female is only responding to environmental conditions because of our restricted sample. Further investigations on larger samples are needed to shed light on the proximate causations and particularly on the motivational processes associated with parental behavior. For example, brood manipulations of nestlings of different age would allow to test if the modification of the female behavior is linked with the activity level of the young.

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BREEDING BIOLOGY OF THE ZONE-TAILED HAWK AT THE LIMIT OF ITS DISTRIBUTION

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ABSTRACT.—Twelve zone-tailed hawk (*Buteo albonotatus*) nest stands in eight territories were studied in northcentral New Mexico during 1990–92 to determine the nesting chronology, nesting habitat, diet, and productivity of a population that is at the limit of the species' distribution. Zone-tailed hawks arrived on the study area from late March to early April and their breeding season ended in mid- to late September when the family unit left the nest stand. All nest stands were in ponderosa pine (*Pinus ponderosa*) forests located in the bottom or on the slopes of steep-walled canyons, and frequently in close proximity to cliffs. Stand basal area averaged 23.8 m²/ha and percent canopy closure averaged 69.2% ($N = 10$). Nest trees ($N = 8$) were large, averaging 23.8 m in height and 59.8 cm diameter at breast height (dbh). The diet consisted of a mixture of mammalian, avian and reptilian prey species that are common in the study area. During 1990 and 1991 only one of six known territories successfully fledged two and one young, respectively. During 1992 two new territories were located and these were the only successful nests (fledged one and two young). Although sample sizes are small, the productivity that we recorded is the lowest reported productivity of any zone-tailed hawk population. Reasons for the low productivity are unknown.

KEY WORDS: *breeding chronology; Buteo albonotatus; diet; habitat; New Mexico; productivity; zone-tailed hawk.*

Biología reproductiva de *Buteo albonotatus* en el límite de su distribución

RESUMEN.—Se estudiaron doce nidos de *Buteo albonotatus* en ocho territorios ubicados en el centro norte de New Mexico, entre 1990 y 1992. Se determinó la cronología y hábitat de nidificación, dieta y productividad de una población que se encuentra en el límite de distribución de la especie. *Buteo albonotatus* llegaron al área de estudio a fines de marzo y a principios de abril y su estación reproductiva finalizó la última quincena de septiembre, cuando la familia dejó el nido. Todos los nidos se localizaron en bosques de *Pinus ponderosa* ubicados en el fondo o sobre laderas de cañones amurallados y frecuentemente cercanos a riscos. El promedio de áreas basales de las agrupaciones vegetales es de 23.8 m²/ha y el porcentaje promedio de la cobertura del dosel es de 69.2% ($N = 10$). Los nidos se encontraban ubicados en árboles a una altura promedio de 23.8 m y 59.8 cm dbh ($N = 8$). La dieta consistió de una mezcla de presas de mamíferos, aves y reptiles que son comunes en el área de estudio. Durante 1990 y 1991, solamente uno de los seis territorios conocidos produjo dos y un volantones, respectivamente. Durante 1992 dos nuevos territorios fueron localizados con una producción de un y dos volantones. Aunque el tamaño de la muestra es pequeño, la productividad registrada es la más baja reportada para una población de *B. albonotatus*. Razones para esta baja productividad son desconocidas.

[Traducción de Ivan Lazo]

The zone-tailed hawk (*Buteo albonotatus*) is a relatively uncommon and widely distributed raptor of the southwestern United States and Latin America (Brown and Amadon 1968, Palmer 1988). Only

about five percent of its range is in the U.S., and it has been estimated that only 80–100 nest stands of this species are known in this region (Millsap 1981, Snyder and Glinski 1988). In the U.S., the zone-

tailed hawk is most commonly found in southern and central Arizona and New Mexico, although nesting pairs have been documented in Texas and southern California (Oberholser and Kincaid 1974, Matteson and Riley 1981, Snyder and Glinski 1988). It is most commonly found in mountainous areas and lowland riparian zones, and is often associated with steep terrain. Nest-stand vegetation is varied, but deciduous riparian and montane coniferous forests are the most common types reported. The zone-tailed hawk is a year-round resident in lower latitudes but is thought to be migratory throughout the northern third of its range, though winter sightings in this area are not uncommon (Palmer 1988). Limited information is available on the species' breeding biology (Matteson and Riley 1981, west Texas; Millsap 1981, westcentral Arizona; Hiraldo et al. 1989, Durango, Mexico), and no published information is available on the ecology of zone-tailed hawk populations at northern range boundaries.

In this paper, we describe characteristics of the breeding biology of zone-tailed hawks nesting in coniferous forests in northcentral New Mexico that we observed during the 1990–92 breeding seasons. This population is at the extreme northern border of the species' range. We estimated the density of nesting pairs in one portion of the study area and annual reproductive success. We also described the breeding chronology, nest-stand characteristics, and nesting season diet of the zone-tailed hawk in this area.

STUDY AREA

The study was conducted in the Jemez Mountains and adjacent Pajarito Plateau of northcentral New Mexico. This area is characterized by rough terrain dissected by steep-walled canyons at regular intervals. The vegetation at higher elevations is dominated by ponderosa pine (*Pinus ponderosa*) and mixed conifer forests, with pinyon-juniper woodland dominating the lower elevations. Drainages contain riparian habitats dominated by Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine, with cottonwoods (*Populus* spp.) present at lower elevations. The vegetative characteristics of this area are described in detail in Kennedy (1991). This area encompasses approximately 650 000 ha and is managed primarily by the U.S. Forest Service, Santa Fe National Forest, the U.S. Park Service, Bandelier National Monument (BNM), and Los Alamos National Laboratory.

METHODS

Nest Searches, Breeding Chronology and Productivity. Prior to the 1990 nesting season, we collected all available information on historical occurrences of the zone-tailed hawks in the study area. This database included

information collected from the New Mexico Ornithological Society (NMOS) nest cards, a local ornithological society (Pajarito Ornithological Society), and entries in the wildlife sightings database from BNM (C. Allen pers. comm.), as well as records from professional biologists (D. Crowe unpubl. data, T. Johnson unpubl. data, P.L. Kennedy unpubl. data). We used this database to design nest surveys and as preliminary information on the nesting chronology of the zone-tailed hawk in the study area.

During July to August 1990, July to September 1991 and from 22–29 July in 1992, all historically active nest stands and areas of frequent sightings were searched for signs of zone-tailed hawk nesting activity and to estimate reproductive success (number of bandable young). Road and foot surveys and taped broadcasts of conspecific calls were used in these areas to aid in the detection of nesting hawks. In July 1991, an exhaustive search of BNM (13 254 ha) was conducted for active nests to estimate the density of breeding territories in an area with minimal human-induced landscape alterations. All forested habitats were searched with equal effort.

Nest Stand Habitat. The dominant vegetation type, as characterized by the canopy species, and general topographic features were recorded at all nest stands ($N = 12$). A nest stand is defined as the area surrounding a nest tree, including vegetative and topographic features used by a nesting pair during the entire nesting season exclusive of foraging areas. Elevation and topographic location were determined from nest locations plotted on 7.5 min U.S. Geological Survey maps. The basal area (BA; m^2/ha) and percent canopy closure (% CC) were measured at five points in nine of the 12 nest stands. These points were the nest tree, and points 50 m from the nest tree in each of the cardinal directions. The stand % CC and BA are presented as the average of the five measurements. The BA of each canopy species was measured with a Relaskop using a basal area factor of two (Wenger 1984) and % CC was measured with a convex spherical densiometer (Lemmon 1956, 1957). The aspect of the nest stand was measured at 10 of the 12 nest trees. Nest tree height (m), and diameter at breast height (dbh [cm]) were measured at eight nest trees, and nest height, aspect of the nest structure, and the location of the nest within the nest tree was recorded when the nest structures were still present ($N = 7$). All height measurements were made with a clinometer.

Diet. Prey remains and castings were collected at least twice at each occupied nest stand (any site where at least one adult exhibited nesting behavior, i.e., defensive vocalizations, addition of greenery to nest structures) during 1990 and 1991. Prey remains collected at four nests from 1986–90 in the course of other raptor studies were included in the analysis of prey items. Remains were identified to genus and species when possible, and a sample of the castings collected were analyzed for the presence of reptilian, avian, and mammalian prey.

In addition, prey deliveries were monitored for 2–3 d/wk for 5 wk (July to early August; last week of the nestling period and the first 4 wk of the fledgling-dependency period) at Nest 1 which was the only nest in the study area that successfully produced nestlings during both 1990 and 1991. During both years, Nest 1 was monitored

by one observer (DC) for 4–12 hr each day with a Celestron C90 telescope. The observer was in a blind located approximately 200 m up slope from the nest tree. Prey delivery rates were calculated for each sample period and converted to daily rates assuming 13.5 hr/d which is the average daylength in this area during July and early August (Kennedy 1991).

RESULTS AND DISCUSSION

Nest Searches. A total of 10 nests were located in six territories (Nests 1–6) on this study site during 1990 and 1991. We assumed that three of the territories (Nests 2, 4, and 6) contained alternate nest stands. This assumption was based on the close proximity of the alternate nests (<2 km) and the absence of simultaneous occupancy during a breeding season. In 1992 two additional nest stands (Nests 7 and 8) on two territories were located.

Nesting Density. Two occupied nest stands (Nests 3 and 4) were located in BNM during the 1991 exhaustive survey. Nesting density, based on the two occupied nests, is estimated to be roughly one pair/6 627 ha or 1.51 pairs/100 km². This density estimate is based on the untested assumption that all occupied sites were located during the survey. Also, because of the small sample size of nests we cannot assume that this density estimate is representative of the nesting density throughout the study area.

Snyder and Glinski (1988) report that zone-tailed hawk nests are rarely closer together than 16 km. How they arrived at that conclusion is not evident in their review paper. However, our results do not support that generalization. The minimum distance between two active nests in our study was 3.6 km and the average nearest neighbor distance was 5.4 km (± 2.0 km; $N = 8$). The differences between our results and their conclusions may be attributed to differences in densities of linear riparian habitat as compared with contiguous montane ponderosa pine forests.

Breeding Chronology. Zone-tailed hawks have been observed on our study site as early as the last week in March, and have been recorded regularly during early April (T. Johnson pers. comm., BNM wildlife sightings database). These data suggest that the zone-tailed hawk probably arrives in the breeding area in northcentral New Mexico between late March and mid-April. The first sightings of birds in this study area are consistent with reported arrival dates in other areas (Millsap 1981, Palmer 1988).

Two courtship displays for this species have been

reported: high-circling with occasional flapping and calling (Palmer 1988), and sky-dancing (Oberholser and Kincaid 1974). We observed these displays in late April 1985, late May 1986, and in early August 1990. Courtship likely begins when both adults arrive in their territory and apparently continues throughout the breeding season. The courtship period is still poorly understood, and dates of courtship activity in this species are poorly documented.

Using an estimated incubation period of 35 d (Newton 1979) and back dating from the date we observed fledging, the approximate date of egg laying at Nest 1 was 1 May in 1990, and between 1–7 May in 1991. These dates are also consistent with reports of egg-laying in other areas, which range from 29 March to 17 May (Millsap 1981, Palmer 1988). The hatch dates in our study area, as determined from estimates of nestling ages and observed fledging dates at Nest 1, are estimated to be in the first week of June in 1990, and between 4 and 11 June in 1991. Millsap (1981) found that over 50% of eggs in southeastern Arizona hatched by 10 June and all nests had hatched by 27 June.

The young that we observed at Nest 1 remained in the nest for 38–42 d. This observation is consistent with Newton's (1979) report of a 35–42 d nestling period. The young left Nest 1 on 12 and 15 July of 1990 and 1991, respectively. The first prolonged flight by the young was on 20 July 1990 and 30 July 1991 when they were approximately 6–8 wk old. The young at the two successful nests in 1992 (Nests 7 and 8) had recently fledged when we conducted our nest surveys in late July. Millsap (1981) reported that 50% of zone-tailed hawks in westcentral Arizona had fledged by 28 July, and all had fledged by 10 August. For one nest in Durango, Mexico, Hiraldo et al. (1989) reported a fledging date of July 17.

The end of the fledgling-dependency period was not observed in 1990 or 1992, but in 1991, the fledglings were last observed in the Nest 1 stand with an adult on 12 September. This corresponds with a fledgling-dependency period of approximately 8 wk. Hiraldo et al. (1989) reported a fledgling-dependency period of 4 wk for a nest in Durango, Mexico. The length of this period is probably quite variable and is difficult to estimate from observations of only two nests and no radio-telemetry data on juveniles.

Between 12 and 28 September 1991 all family members left the Nest 1 stand. This is again in

agreement with information on departure dates observed in westcentral Arizona, where all territories were unoccupied by 3 October (Millsap 1981). There have been no observations of zone-tailed hawks in the study area after late September.

Nest Stand Habitat. Similar to Millsap's (1981) observations in westcentral Arizona, all of the 12 nest stands we located were in the bottom or on the slopes of steep-walled canyons and frequently in close proximity to cliffs. The dominant vegetation in all nest stands was ponderosa pine/oak (*Quercus* spp.) or ponderosa pine/douglas fir/oak. Although riparian habitat occurs in the study area, no nest stands were located in this habitat type. This is in contrast with Millsap's (1981) study area where 92.8% ($N = 26$) of the nest stands were in deciduous riparian forests and 7.2% ($N = 2$) were in ponderosa pine forests. These study area differences in nest stand habitat are probably a result of differences in nesting habitat availability. For example, montane conifer forest communities were 0.3% of Millsap's (1981) study area and 43.7% of our study area (M.S. Siders and P.L. Kennedy unpubl. data). Deciduous riparian forests were the most abundant forested habitat in Millsap's (1981) study area (0.8% of study area). We do not have estimates of deciduous riparian forest availability in our study area but it is considerably less abundant than the montane conifer communities.

All nest stands were between 1936 and 2316 m in elevation. In westcentral Arizona most zone-tailed hawk nest stands were above 1100 m elevation (Millsap 1981). Stand basal area averaged 23.8 m²/ha (SD = 3.4) and % CC averaged 69.2% (SD = 6.5). No comparable habitat data are available from other study areas.

All of the nest trees were ponderosa pine and the average height and dbh of the nest trees were 23.8 m (SD = 6.0) and 59.8 cm (SD = 9.1), respectively. The two ponderosa pine nest trees measured by Millsap (1981) were comparable in size to those we measured averaging 22.9 m (SD = 1.2) in height and 63.5 cm (SD = 0.4) in diameter. Eight of 11 nest stands in the Big Bend area of west Texas were also in ponderosa pine but no nest stand measurements are available for these sites (S. Matteson et al. unpubl. data in Snyder and Glinski 1988).

The nest structures were all located in the upper portion of the canopy ($\bar{x} = 90.6\%$ [SD = 0.04] of the tree height) at an average height of 22.9 m (SD =

5.1). Millsap (1981) reported nest heights of 19.8 m (SD = 0.3, $N = 2$). The aspects of the nests in this study were west ($N = 5$), north ($N = 1$), or east ($N = 1$), and the structures were constructed of sticks and lined with greenery. No comparable nest aspect data are available from other study areas.

Diet. Remains from 26 prey items were collected and identified (Nests 1 and 3–5) and 26 of 105 castings were analyzed (Nests 1 and 3–5). In addition, a total of 84 prey deliveries were observed at Nest 1 (52 in 1990; 32 in 1991) during a total of 175.5 hr of observation (87.5 in 1990; 88 in 1991). Table 1 summarizes the diet data collected at Nest 1 where all three methods of diet analysis were used. Table 2 is a list of the prey taxa used by zone-tailed hawks during the nesting season in our study area. It is a composite list based on all three dietary methods and all diet samples.

At Nest 1, reptiles accounted for 26.2, 0, and 87.5% of deliveries, prey remains, and castings, respectively. Mammalian taxa accounted for 41.7, 27.3, and 87.5% of deliveries, prey remains, and castings, and avian taxa accounted for 23.8, 72.7, and 81.3% of deliveries, remains, and castings, respectively (Table 1). The discrepancy between the occurrence of reptiles in deliveries, remains and castings at Nest 1 may result from the tendency of zone-tailed hawks to entirely consume reptilian prey, leaving few remains. This may result in reptiles being underrepresented in raptor diets (Marti 1987, Rosenberg and Cooper 1990). Avian prey are probably overrepresented in remains because of the visibility of their remains (Marti 1987, Rosenberg and Cooper 1990).

Thirteen genera/species were identified in the diet (Table 2). Our data and food habits data collected in other studies (Snyder and Wiley 1976, Sherrod 1978, Millsap 1981, Hiraldo et al. 1991) indicate that the zone-tailed hawk has a broad diet, including many vertebrates and some invertebrates. All populations take a mix of mammals, birds, and herpetofauna, but as expected, the percentage of these taxa in the diet varies between populations. The variation is probably a function of sampling method, nest sample size and local prey availability in a variety of habitat types.

The average prey delivery rates at Nest 1 in 1990 and 1991 were 8.0 prey/d (SD = 2.8; $N = 12$ d) and 4.8 prey/d (SD = 2.5; $N = 9$ d), respectively. The differences in the rates between years are prob-

Table 1. Dietary data collected at the only successful zone-tailed hawk nest (Nest 1) in the Jemez Mountains, New Mexico during 1990 and 1991.

METHOD	N ^a	PREY TAXA	% OF DIET ^b
Prey deliveries	22	Reptiles	26.2
	14	<i>Crotaphytus</i> sp.	16.7
	1	<i>Sceloporus</i> sp.	1.2
	7	Unidentified Lizard	8.3
	20	Birds	23.8
	2	<i>Colaptes auratus</i>	2.4
	1	<i>Aphelocoma coerulescens</i>	1.2
	1	<i>Turdus migratorius</i>	1.2
	2	Tanager-size bird	2.4
	5	<i>Loxia curvirostra</i>	5.9
	8	Finch-size bird	9.5
	1	Unidentified birds	1.2
	35	Mammals	41.7
	33	<i>Tamias</i> sp.	39.3
	2	<i>Sciurus variegatus</i>	2.4
	7	Unidentified Prey	8.3
	Total		100.0
Prey remains	0	Reptiles	0.0
	8	Birds	72.7
	1	<i>Chordeiles minor</i>	9.1
	2	<i>Colaptes auratus</i>	18.2
	1	<i>Cyanocitta stelleri</i>	9.1
	1	Unidentified jay	9.1
	1	<i>Loxia curvirostra</i>	9.1
	2	Finch-size bird	18.2
	3	Mammals	27.3
	1	<i>Sylvilagus</i> sp.	9.1
	2	<i>Tamias</i> sp.	18.2
	Total		100.0
Castings	14	Reptiles	87.5
	13	Birds	81.3
	14	Mammals	87.5
Total	16		100.0

^a N is the number of deliveries, prey remains, or castings in which each taxa is represented. All samples were collected during 1990 and 1991.

^b For the prey deliveries and prey remains this represents the percent of individuals observed. For the castings this represents the percent of the castings in which each taxon is represented.

ably due to differences in number of young being fed (two in 1990 and one in 1991). Hiraldo et al. (1989) reported a mean prey delivery rate of 5.9 prey/d (SD = 2.8; N = 10 d) during the post-fledging period at a zone-tailed hawk nest in Durango, Mexico where two young fledged.

Most of the prey were delivered midday between 09:00 and 17:00 H during both years (90.4% of total deliveries in 1990 and 78.1% in 1991). This diurnal pattern probably reflects the activity patterns of some

of its principal prey, lizards and medium-sized diurnal mammals (Table 1) which are more active during the warmer portions of the day in this study area (P.L. Kennedy and J.L. Morrison unpubl. data).

At Nest 1, the smaller parent (presumably the male) made almost all of the prey deliveries (93.8% in 1990 and 96.8% in 1991) and the majority of these deliveries (83.3% and 93.5% in 1990 and 1991, respectively) were brought directly to the nest without a transfer to the larger parent (presumably the

Table 2. Prey taxa^a of zone-tailed hawks nesting in the Jemez Mountains, New Mexico during 1990 and 1991.

TAXA	NO. NESTS ^b
Reptiles	
<i>Crotaphytus</i> sp.	2
<i>Sceloporus</i> sp.	1
Birds	
<i>Chordeiles minor</i>	1
<i>Colaptes auratus</i>	1
<i>Cyanocitta stelleri</i>	1
<i>Aphelocoma coerulescens</i>	1
<i>Turdus migratorius</i>	1
<i>Loxia curvirostra</i>	2
Mammals	
<i>Sylvilagus</i> sp.	1
<i>Tamias</i> sp.	2
<i>Sciurus variegatus</i>	1
<i>Sciurus aberti</i>	1
<i>Peromyscus</i> sp.	1

^a Prey taxa were identified from observations of prey deliveries at Nest 1 during 1990–91 or analyses of prey remains collected at all occupied nests from 1986–91.

^b Number of occupied territories where this taxon was observed in either a prey remain or prey delivery during 1986–91.

female) upon entering the nest stand. The female was in the nest stand throughout most of the observation period but her primary role in food provisioning was to feed the prey to the nestlings after the male delivered it to the nest. She apparently was not involved in food provisioning after the young were self-feeding. As Hiraldo et al. (1989) suggest, the zone-tailed hawk, like other raptors, appears to have sex role partitioning during brood rearing.

Reproductive Success. The 1990–92 reproductive success of the zone-tailed hawk in the Jemez Mountains was low. Four of six territories were occupied in 1990–91 and five of eight territories in 1992. In 1990 and 1991 one territory (Nest 1) produced two and one young, respectively, and in 1992 two territories (Nests 7 and 8) produced three young in total. The average reproductive success for the three years was 0.45 yg/occupied territory (SD = 0.18).

The low reproductive success observed in 1990–92 is probably an accurate representation of the population productivity during this period and not anomalous. The first successful nesting attempt re-

corded in this area occurred in 1985 and that nesting territory has not successfully produced young since that year. Another nest successfully fledged young in 1989, but has been unsuccessful since. The one nest that was successful in both 1990 and 1991 was successful for six consecutive years (1986–91) but failed prior to hatching in 1992, and failed in the nestling period in 1993 (T. Dean unpubl. data).

In west Texas, Matteson and Riley (1981) reported productivity of 1.14 young/occupied territory in 1975 and 0.77 young/occupied territory in 1976. The average reproductive success for 1979 and 1980 in westcentral Arizona (Millsap 1981) was 1.9 yg/occupied territory (SD = 0.71). Although sample sizes are small, the productivity that we recorded is the lowest reported productivity of any zone-tailed hawk population. In the absence of survival and immigration rate data, we cannot evaluate if this rate of reproduction is sufficient to sustain this population.

The reason for the low productivity in this population during 1990–92 is unclear. It might be an artifact of the small sample size or some unidentified local factor that influenced the 1990–92 nest success, such as low food availability and/or high nest predation. However, populations at range margins generally exhibit lower productivity and survivorship than populations nearer the center of a species' range, and such outlying populations may serve as a sink for surplus individuals from central populations (Newton 1979, Snyder and Glinski 1988, Howe et al. 1991). These outlying populations may not be capable of producing enough offspring to replace adults, and such populations may only remain intact as long as there is a surplus of individuals from centrally located populations that regularly disperse to such 'sink' populations (Pulliam 1988, Howe et al. 1991). Populations such as the one we observed may be located in areas of marginal habitat that only allows for successful reproduction in exceptional years.

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PARASITIC HELMINTHS OF SIX SPECIES OF HAWKS AND FALCONS IN FLORIDA

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ABSTRACT.—Six species of hawks and falcons collected in Florida were examined for helminth parasites from 1971–87. A total of 38 helminth species (15 digeneans, one cestode, 20 nematodes, and two acanthocephalans) was recovered from the red-shouldered hawk (*Buteo lineatus*), red-tailed hawk (*Buteo jamaicensis*), broad-winged hawk (*Buteo platypterus*), sharp-shinned hawk (*Accipiter striatus*), Cooper's hawk (*Accipiter cooperii*), and American kestrel (*Falco sparverius*). The red-shouldered hawk harbored the most species per infected host ($\bar{x} = 5.8$) while the American kestrel harbored the least ($\bar{x} = 1.7$). One helminth species was classified as a host specialist and 16 species as generalists in raptors. Euryphagic host species such as the red-shouldered hawk and broad-winged hawk harbored more helminth species than more specialized feeders such as the red-tailed hawk and Cooper's hawk. Helminths were not implicated as the cause of death in any of the hosts examined.

KEY WORDS: *falcons; Florida; hawks; helminths; parasites.*

Helminthos parásitos de seis especies de aguiluchos y halcones en Florida

RESUMEN.—Seis especies de aguiluchos y halcones colectados en Florida, fueron examinados en busca de parásitos helmintos desde 1971 a 1987. Un total de 38 especies de helmintos (15 digeneanos, un cestódo, 20 nemátodos y dos acantocéfalos) fueron obtenidos de *Buteo lineatus*, *Buteo jamaicensis*, *Buteo platypterus*, *Accipiter striatus*, *Accipiter cooperii* y *Falco sparverius*. *Buteo lineatus* albergó la mayoría de las especies por hospedero infectado ($\bar{x} = 5.8$). Una especie de helminto fue clasificada como especialista y 16 especies como generalistas en rapaces. Los helmintos no estuvieron implicados en las causa de muerte de ninguno de los especímenes examinados.

[Traducción de Ivan Lazo]

Perhaps because of their protected status under federal law, very little information is available on the parasites of hawks in the United States. Most early studies on raptor helminths focused on the taxonomy of specific groups such as trematodes (Denton and Byrd 1951, Schell 1957, Dubois and Rausch 1950), cestodes (Freeman 1959), nematodes (Schell 1953), or acanthocephalans (Nickol 1983). A report by Taft et al. (1993) on the helminths of 10 species of hawks in Minnesota and Wisconsin is the only paper which lists the overall prevalences and intensities of helminths in hawks in North America.

Since 1971, a large number of dead or dying raptors have been submitted to the Department of Infectious Diseases at the University of Florida, Gainesville, for determination of the cause of death.

In this paper we report on the helminths of six species of hawks and falcons.

Methods

Sixty-one birds obtained from 19 counties in Florida between December 1971 and March 1987, were examined. Causes of death included collisions with vehicles, collisions with wires, poisoning, and gunshot wounds. Most birds were found dead, but a small, number of birds found alive with injuries too severe to be treated had to be euthanized. Carcasses were frozen within 4 hr of collection or death, transported to the laboratory, and later thawed and examined at necropsy.

Techniques for recovering, fixing, staining, and examining helminths followed Kinsella and Forrester (1972). Terminology follows Margolis et al. (1982) with prevalence defined as the number of individuals of a host species infected with a parasite species divided by the number of hosts examined, and mean intensity defined as the total number of individuals of a parasite species divided by the number of hosts infected with that species. Voucher specimens of helminths were deposited in the Harold W. Manter Laboratory of the University of Nebraska State Museum (Accession Nos. 36883–36894, 36896–36906, 36930–36932).

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RESULTS AND DISCUSSION

Thirty-eight species of helminths (15 digeneans, one cestode, 20 nematodes, and two acanthocephalans) were found. In Table 1 the prevalences and intensities of infection of helminths from the red-shouldered hawk (*Buteo lineatus*), red-tailed hawk (*Buteo jamaicensis*), and broad-winged hawk (*Buteo platypterus*) are listed. The same data for the sharp-shinned hawk (*Accipiter striatus*), Cooper's hawk (*Accipiter cooperii*), and American kestrel (*Falco sparverius*) are given in Table 2. The number of helminth species per infected host varied from one to eleven ($\bar{x} = 2.5$), with 19 birds free from helminths. In Table 3 we give the number of species per host for the four hosts with sample sizes of five or more. The red-shouldered hawk harbored the most species with a mean of 5.8 species per infected bird (range 1–9), while the kestrel averaged only 1.7 species with no bird having more than three species. The red-tailed hawk and sharp-shinned hawk were intermediate between these extremes.

No one species of helminth was found in all six hosts. Three species of intestinal digeneans (*Strigea falconis*, *Neodiplostomum americanum*, *N. attenuatum*) and one species of nematode (*Procyrnea mansonii*) were found in five host species. Nematodes identified as *Physaloptera* sp. were found also in five host species, but many were larvae or immature adults and may represent more than one species. No species demonstrated the high prevalences and intensities usually associated with the concept of "core" species in helminth communities (Bush and Holmes 1986).

Previous workers on helminth communities in lesser scaup (*Aythya affinis*; Bush and Holmes 1986) and shorebirds (Edwards and Bush 1989) have categorized helminth species as specialists, generalists, or cosmopolitan. Specialists were defined narrowly as having the bulk of reproducing adults found only in a single host species or having been reported from a single host species. Generalists are those reported from a wide variety of related species, and cosmopolitan species those found in at least two vertebrate classes.

By these definitions, only one species found in Florida, *Parastrigea tulipoides*, can be considered a host specialist. This species was described from the red-shouldered hawk in North Carolina by Miller and Harkema (1965) and was also found in Florida only from the red-shouldered hawk. Two species can be considered as cosmopolitan: *Echinostoma tri-*

volvis, reported from many species of birds as well as muskrats (Huffman and Fried 1990), and *Baschkirovitrema incrassatum*. Our record of *B. incrassatum* in a red-shouldered hawk is extremely unusual since this trematode has been reported previously only from otters (*Lutra* spp.) in Europe and North America (Forrester 1992).

The remaining species could be classified as host generalists. This category could be subdivided into raptor generalists, reported from a variety of hawks (and occasionally owls), but not other birds; and true generalists, reported from other orders of birds, including waterfowl and passerines. In Table 4 we list helminth species by category, with 16 classified as raptor generalists and nine as generalists in birds. Helminths not identified to species were excluded because their host relationships were unknown.

Cestodes were extremely rare in our sample, restricted to single infections of *Cladotaenia globifera* in a red-tailed hawk and a broad-winged hawk. Freeman (1959) found only 12 of 2350 rodents that can serve as intermediate hosts infected with this tapeworm in Canada. No infections of *C. globifera* have been found in 714 Florida rodents of five species (Kinsella 1974, 1988, 1991), so population densities in intermediate hosts appear to be even lower than in Canada.

Hawks are one of the few groups of birds that are hosts to both subgenera of the nematode genus *Tetrameres*, which parasitize the proventricular glands. The species of the subgenus *Tetrameres* that we found in the red-shouldered hawk appears to be the same as that described by Mollhagen (1976) from the same host. However, since Mollhagen's dissertation was never published, the species has no taxonomic validity. We also found an undescribed species of the subgenus *Microtetrameres* in the red-shouldered hawk and Cooper's hawk.

Bosakowski and Smith (1992) studied the comparative diets of sympatric raptors in the eastern deciduous forest, including four of the hawks we studied (red-shouldered, red-tailed, broad-winged, Cooper's). The red-shouldered hawk exhibited the greatest food-niche breadth, including in its diet frogs, turtles, fish, crayfish, and small mammals. Its euryphagic diet undoubtedly contributes to the richness of its helminth fauna in comparison to that of the other hawks. The broad-winged hawk was nearly as euryphagic as the red-shouldered hawk, and, although only one broad-winged hawk was examined in this study, it harbored 11 species of helminths.

Table 1. Parasitic helminths from red-shouldered, red-tailed, and broad-winged hawks in Florida.

HELMINTH	BUTEO LINEATUS N = 18						BUTEO JAMAICENSIS N = 13						BUTEO PLATYPTERUS N = 1					
	PREVALENCE			INTENSITY			PREVALENCE			INTENSITY			PREVALENCE			INTENSITY		
	HOST	INF.	%	MEAN	RANGE	LOCA- TION IN	HOST	INF.	%	MEAN	RANGE	LOCA- TION IN	HOST	INF.	%	MEAN	RANGE	LOCA- TION IN
Trematoda																		
<i>Strigea falconis</i> (Szidat 1928)	SI	—	—	—	—	SI	8	62	447	18–1579	1	100	16	16	16	16	16	16
<i>Neodiplostomum americanum</i> (Chandler & Rausch 1947)	SI	3	17	160	35–234	SI	3	23	4	1–7	1	100	1	1	100	1	1	1
<i>Neodiplostomum attenuatum</i> (Linstow 1906)	SI	10	56	102	6–1022	SI	6	46	66	7–228	1	100	1	100	165	165	165	165
<i>Neodiplostomum pearsoni</i> (Dubois 1962)	SI	—	—	—	—	SI	—	—	—	—	1	100	1	100	5	5	5	5
<i>Ophiosoma microcephalum</i> (Szidat 1928)	SI	6	33	182	2–461	SI	2	15	4	1–7	—	—	—	—	—	—	—	—
<i>Parastrigea tulipoides</i> (Miller & Harkema 1965)	SI	4	22	7	2–15	SI	—	—	—	—	—	—	—	—	—	—	—	—
<i>Platynosomum illiciens</i> (Braun 1901)	L	1	6	7	7	L	—	—	—	—	—	—	—	—	—	—	—	—
<i>Brachylecithum rarum</i> (Travassos 1917)	L	5	28	7	3–18	L	—	—	—	—	—	—	—	—	—	—	—	—
<i>Baschkirovitrema incrassatum</i> (Diesing 1850)	SI	1	6	15	15	SI	—	—	—	—	—	—	—	—	—	—	—	—
<i>Microparaphium facetum</i> (Dietz 1909)	C	2	11	2	1–2	C	—	—	—	—	—	—	—	—	—	—	—	—
<i>Echinoparyphium</i> sp.	SI	—	—	—	—	SI	1	8	1	1	—	—	—	—	—	—	—	—
Cestoda																		
<i>Cladotaenia globifera</i> (Batsch 1786)	SI	—	—	—	—	SI	1	8	10	10	1	100	2	2	100	2	2	2
Nematoda																		
<i>Capillaria falconis</i> (Goeze 1782)	SI	10	56	2	1–7	SI	4	31	5	1–12	—	—	—	—	—	—	—	—
<i>Capillaria contorta</i> (Creplin 1839)	E	4	22	1	1–2	E	2	15	3	1–4	—	—	—	—	—	—	—	—
<i>Cyathostoma americana</i> (Chapin 1925)	T	—	—	—	—	T	1	8	1	1	—	—	—	—	—	—	—	—
<i>Desportesius invaginatus</i> (Linstow 1901)	E	—	—	—	—	E	3	23	3	1–5	1	100	4	4	100	4	4	4
<i>Synhimantus hamatus</i> (Linstow 1877)	P	10	56	10	1–48	P	5	38	1	1–2	1	100	12	12	100	12	12	12
<i>Synhimantus</i> sp.	P	1	6	1	1	P	—	—	—	—	—	—	—	—	—	—	—	—
<i>Procyrnea mansioni</i> (Seurat 1914)	E, P	1	6	1	1	E, P	3	23	2	1–2	1	100	1	1	100	1	1	1
<i>Tetrameres (M.) accipiter</i> (Schell 1953)	P	—	—	—	—	P	3	23	37	3–103	—	—	—	—	—	—	—	—
<i>Tetrameres (M.)</i> sp.	P	1	6	3	3	P	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tetrameres (T.)</i> sp.	P	7	39	3	1–20	P	—	—	—	—	—	—	—	—	—	—	—	—
<i>Porrocaecum depressum</i> (Zeder 1800)	SI	—	—	—	—	SI	4	31	9	1–30	—	—	—	—	—	—	—	—
<i>Porrocaecum angusticolle</i> (Molin 1860)	SI	—	—	—	—	SI	—	—	—	—	1	100	23	23	100	23	23	23
<i>Physaloptera</i> sp.	P	2	11	2	1–2	P	1	8	2	2	—	—	—	—	—	—	—	—
<i>Gnathostoma</i> sp.	E	1	6	1	1	E	—	—	—	—	—	—	—	—	—	—	—	—
Larval spirurids	E, P	9	50	2	1–8	E, P	3	23	17	1–50	—	—	—	—	—	—	—	—
Acanthocephala																		
<i>Centrorhynchus kuntzi</i> (Schmidt and Neiland 1966)	SI	14	78	9	1–21	SI	4	31	13	3–28	1	100	11	11	100	11	11	11
Larval acanthocephalan	E	1	6	1	1	E	—	—	—	—	—	—	—	—	—	—	—	—

^a C = cloaca, E = esophagus, L = liver, P = proventriculus, SI = small intestine, T = trachea

Table 2. Parasitic helminths from American kestrels, sharp-shinned hawks, and Cooper's hawks in Florida.

HELMINTH	LOCAL- TION	FALCO SPARVERIUS N = 22				ACCIPITER STRIATUS N = 5				ACCIPITER COOPERII N = 2			
		PREVALENCE	INTENSITY	MEAN RANGE	PREVALENCE	INTENSITY	MEAN RANGE	PREVALENCE	INTENSITY	PREVALENCE	INTENSITY	MEAN RANGE	INTENSITY
	IN HOST	INF.	%		INF.	%		INF.	%	INF.	%		
Trematoda													
<i>Strigea falconis</i> (Szidat 1928)	SI	1	5	1	—	—	—	1	20	1	50	30	30
<i>Neodiplostomum americanum</i> (Chandler & Rausch 1947)	SI	—	—	—	—	—	—	4	80	1	50	93	93
<i>Neodiplostomum attenuatum</i> (Linstow 1906)	SI	—	—	—	—	—	—	2	40	2	100	4	2-6
<i>Neodiplostomum pearsoni</i> (Dubois 1962)	SI	—	—	—	—	—	—	1	20	—	—	—	—
<i>Ophiosoma microcephalum</i> (Szidat 1928)	SI	—	—	—	—	—	—	—	—	1	50	9	9
<i>Parastrigea campanula</i> (Dubois and Rausch 1950)	SI	—	—	—	—	—	—	1	20	—	—	—	—
<i>Platynosomum illiciens</i> (Braun 1901)	L	1	5	4	4	—	—	—	—	—	—	—	—
<i>Brachylecithum nanum</i> (Denton and Byrd 1951)	L	3	14	3	2-4	—	—	—	—	—	—	—	—
<i>Echinostoma trivolvis</i> (Cort 1914)	LI	1	5	1	1	—	—	—	—	—	—	—	—
<i>Prosthogonimus ovatus</i> (Rudolphi 1803)	C	2	9	3	1-5	—	—	—	—	—	—	—	—
Nematoda													
<i>Capillaria falconis</i> (Goeze 1782)	SI	1	5	1	1	—	—	—	—	—	—	—	—
<i>Capillaria</i> sp.	SI, LI	—	—	—	—	2	40	2	—	2	100	2	2-3
<i>Cyathostoma americana</i> (Chapin 1925)	T	—	—	—	—	—	—	—	—	1	50	1	1
<i>Synhimantus hamatus</i> (Linstow 1877)	P	—	—	—	—	—	—	—	—	2	100	3	3
<i>Dispharynx nasuta</i> (Rudolphi 1819)	P	8	36	28	1-125	—	—	—	—	—	—	—	—
<i>Procyrnea mansioni</i> (Seurat 1914)	E, P	4	18	1	1	2	40	1	—	—	—	—	—
<i>Cyrnea semilunaris</i> (Molin 1860)	P	1	5	1	1	—	—	—	—	—	—	—	—
<i>Procyrnea</i> sp.	P	1	5	10	10	—	—	—	—	—	—	—	—
<i>Tetrameres (M.) accipiter</i> (Schell 1953)	P	—	—	—	—	2	40	2	1-3	—	—	—	—
<i>Tetrameres (M.)</i> sp.	P	—	—	—	—	—	—	—	—	1	50	1	1
<i>Porrocaecum depressum</i> (Zeder 1800)	SI	—	—	—	—	—	—	—	—	1	50	2	2
<i>Cardiofilaria pavalovskyi</i> (Strom 1937)	BC	5	23	5	1-18	—	—	—	—	1	50	1	1
<i>Physaloptera</i> sp.	P	2	9	13	8-17	1	20	1	—	—	—	—	—
Larval spirurids	E, P	6	27	5	1-10	—	—	—	—	1	50	1	1
Acanthocephala													
Larval acanthocephalan	E	1	5	1	1	—	—	—	—	—	—	—	—

^a BC = body cavity, C = cloaca, E = esophagus, L = liver, LI = intestine, P = proventriculus, SI = small intestine, T = trachea.

Table 3. Multiple infections in four species of falconiforms from Florida.

NUMBER OF SPEC- IES PER INFECTED HOST	BUTEO			
	LINEATUS N = 18	JAMAI- CENSIS N = 13	ACCIPITER STRIATUS N = 5	FALCO SPARVERIUS N = 22
0	1	2	0	1
1	1	2	1	10
2	0	0	2	7
3	3	2	0	4
4	2	4	1	0
5	1	0	0	0
6	2	0	0	0
7+	8	3	1	0
Mean	5.8	4.7	3.2	1.7

Taft et al. (1993) examined 16 broad-winged hawks from Wisconsin and Minnesota and also found 11 species of helminths.

In contrast, the kestrel averaged only 1.7 species per infected bird, with an almost total absence of the strigeid trematodes characteristic of the other hawks. This finding is confirmed also by Taft et al. (1993), who found only three species of helminths in nine kestrels. The diet of the kestrel consists predominantly of arthropods (Beltzer 1990) and the most prevalent helminth in kestrels, *Dispharynx nasuta*, uses isopods as intermediate hosts. This nematode is more characteristic of galliforms and passeriforms and has been associated with severe proventricular lesions and death (Rickard 1985). The cloacal trematode, *Prosthogonimus ovatus*, also found in Florida only in the kestrel, uses dragonfly naiads as intermediate hosts (Boddeke 1960). Although *P. ovatus* has a broad host range, it has not been reported previously from raptors.

Total helminth intensities in these six species of hawks were comparatively low and no significant lesions were observed. Helminths were not implicated as the cause of death in any of the 75 birds examined. However, species such as *Dispharynx nasuta*, *Tetrameres* spp., and *Centrorhynchus kuntzi* remain as potential pathogens, especially in juvenile birds.

Although sample sizes of hosts were small, it appears unlikely that larger samples of these protected birds will be available in the future. Conclusions concerning host specificity, geographic distribution, and community structure of raptor parasites will

Table 4. Classification of helminth species of raptors in Florida by host specificity.

HELMINTH SPECIES	SPE- CIAL- IST	GENERALIST		COS- MO- POL- ITAN
		RAP- TOR	BIRD	
Trematodes				
<i>Strigea falconis</i>		+		
<i>Neodiplostomum americanum</i>		+		
<i>Neodiplostomum attenuatum</i>		+		
<i>Neodiplostomum pearsoni</i>		+		
<i>Ophiosoma microcephalum</i>		+		
<i>Parastrigea tulipoides</i>	+			
<i>Parastrigea campanula</i>		+		
<i>Platynosomum illiciens</i>		+		
<i>Brachylecithum rarum</i>			+	
<i>Brachylecithum nanum</i>			+	
<i>Baschkirovitrema incrassatum</i>				+
<i>Echinostoma trivolvis</i>				+
<i>Microparyphium facetum</i>			+	
<i>Prosthogonimus ovatus</i>			+	
Cestodes				
<i>Cladotaenia globifera</i>		+		
Nematodes				
<i>Capillaria falconis</i>		+		
<i>Capillaria contorta</i>			+	
<i>Cyathostoma americana</i>		+		
<i>Desportesius invaginatus</i>			+	
<i>Synhimantus hamatus</i>		+		
<i>Dispharynx nasuta</i>			+	
<i>Procyrnea mansioni</i>		+		
<i>Cyrnea semilunaris</i>			+	
<i>Tetrameres accipiter</i>		+		
<i>Porrocaecum depressum</i>		+		
<i>Porrocaecum angusticolle</i>		+		
<i>Cardiofilaria pavlovskyi</i>			+	
Acanthocephala				
<i>Centrorhynchus kuntzi</i>		+		

have to be inferred from limited data. Mauritz Sterner of the University of Nebraska State Museum, Lincoln, is assembling a database of raptor helminths and will accept specimens for deposit. The senior author (J.M.K.) would be happy to identify helminths collected by raptor researchers and deposit specimens in appropriate collections.

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PREY SELECTION BY WILD AMERICAN KESTRELS: THE INFLUENCE OF PREY SIZE AND ACTIVITY

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ABSTRACT.—Based upon previous reports of high visual acuity in falcons, we hypothesized that prey activity influenced prey selection by American kestrels (*Falco sparverius*) more than prey size. Wild, free-ranging kestrels were simultaneously offered one adult (22–30 g, 3.5–4.0 cm in length) and one juvenile (6–12 g, 2.0–2.5 cm in length) brown laboratory mouse (*Mus musculus*). Mice were presented to kestrels on a 1 × 1 m board with a light-green background marked into 10 × 10 cm squares. To prevent escape, each mouse was tethered to a clear strand of monofilament fishing line. Mouse activity was documented by observing the mice through 8× binoculars and recording the behavior of each mouse into a portable cassette recorder. In trials pairing active mice (large or small) with inactive (dead) mice (large or small), kestrels selected active mice 90% of the time. Kestrels also selected the more active of two mice significantly (regardless of size) in trials which we reduced the activity of one mouse, or in trials which one mouse was naturally less active than the other. These results suggest that within the range of prey sizes used in this study, kestrels select prey on the basis of activity, and exhibit little size discrimination in prey choice decisions.

KEY WORDS: *American kestrel; Falco sparverius; prey activity; prey selection; prey size; sexual dimorphism.*

Selección de presa por *Falco sparverius* silvestres: la influencia del tamaño de la presa y su actividad

RESUMEN.—En base a reportes previos de alta agudeza visual en halcones, hipotetizamos que la actividad de la presa influenció la selección de presas por *Falco sparverius*, más que el tamaño de presa. Se ofreció simultáneamente a individuos de *Falco sparverius*, un adulto (22–30 g 3.5–4.0 cm de largo) y un juvenil (6–12 g 2.0–2.5 cm de largo) de la especie *Mus musculus*. Los ratones fueron presentados en una cubierta de color verde claro de 1 × 1 m, marcada en cuadrados de 10 × 10 cm y ubicada sobre la superficie del suelo. Para evitar el escape de los roedores, se amarraron con una fina lienza de pesca. La actividad de los ratones fue documentada por observaciones con binoculares 8× y registro de la conducta de cada individuo en un tocacinta portátil. En ensayos de ratones activos (grandes o pequeños) con inactivos (muertos), *F. sparverius* seleccionó ratones activos el 90% del tiempo. *F. sparverius* también seleccionó el más activo de los dos ratones (sin hacer caso del tamaño) tanto en ensayos donde reducimos la actividad de uno de los ratones como en ensayos en los que un ratón fue naturalmente menos activo que el otro. Estos resultados sugieren que, dentro del rango de tamaño de presa usado en este estudio, *F. sparverius* selecciona la presa sobre la base de su actividad y exhibe poca discriminación por tamaño al hacer su selección.

[Traducción: Walter S. Prexl y Ronald J. Sarno]

Prey selection by North American raptors has received considerable attention (Brown 1965, Metzgar 1967, Mueller 1968, 1971, 1973, Mueller and Berger 1970, Spiegel et al. 1974, Snyder 1975, Ruggiero et al. 1979, Ruggiero and Cheney 1979). But despite our understanding of responses to various prey stimuli in the laboratory, little is known about what factors influence prey choice under more natural conditions (Drye 1980, Smallwood 1981, 1989, Bryan 1984).

Because American kestrels (*Falco sparverius*) normally respond only to live, moving prey and disregard dead prey (Bird and Palmer 1988), prey activity is an obvious important factor of prey choice. Additionally, foraging theory predicts that prey size should also influence prey selection (Schoener 1969). Laboratory studies of screech-owls (*Otus asio*; Marti and Hogue 1979) and loggerhead shrikes (*Lanius ludovicianus*; Slack 1975) demonstrated that these avian predators show distinct prey size preference.

Field studies of kestrel prey selection by Drye (1980) and Bryan (1984) did not account for the activity of mice used in their trials. Although Small-

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wood (1989) found that kestrels selected the larger mouse of a pair, mouse activity was not measured during those trials. When activity was manipulated, however, only one mouse was offered at a time. Thus, it remains unclear how kestrels respond to size and activity when presented with two prey items simultaneously. The reversed sexual dimorphism of kestrels, combined with the sedentary nature of females during the breeding season (Balgooyen 1976), could result in different hunting strategies between the sexes, such as size-dependent prey selection or differences in the propensity to initiate selection and/or number of attacks. The objectives of this study were (1) to assess the relative importance of prey size and prey activity as factors influencing prey selection by male and female American kestrels, and (2) to address potential foraging differences between the sexes.

STUDY SITE AND METHODS

This study was conducted in Washoe and Douglas counties, Nevada, from 15 March 1987 to 15 March 1988. To simulate normal prey activity as much as possible, we used live prey in our experiment. Wild, free-ranging American kestrels were simultaneously offered one adult (22–30 g, 3.5–4.0 cm in length) and one juvenile (6–12 g, 2.0–2.5 cm in length) brown laboratory mouse (*Mus musculus*). Mice were presented to kestrels on a 1 × 1 m light-green board marked into 10 × 10 cm squares. To prevent escape, each mouse was tethered around the pectoral girdle with a strand of clear monofilament line (Smallwood 1981). Each monofilament strand passed through a small hole in the center of the board and was attached to a clothespin on the bottom of the board.

The experiment consisted of three trials. Trial one was designed to test kestrel prey selection for active vs. inactive mice, and small versus large mice. Male and female kestrels were offered either a small active mouse and a large inactive (dead) mouse, or a small inactive (dead) mouse and a large active mouse. Mice were euthanized by an intraperitoneal injection of chlorpromazine (Snyder 1975).

Trial two tested kestrel selection for prey (small vs. large) exhibiting different levels of activity. Kestrels were offered either a normally active large mouse and an artificially less-active small mouse, or a normally active small mouse and an artificially less-active large mouse. Mouse activity was manipulated by attaching a long tether (40 cm) to the designated normally active mouse, thus increasing its radius of travel compared to the short tethered (10 cm), artificially less active mouse. Besides reducing the radius of travel, the short tether inhibited mouse activity. The mouse with the short tether was less active in all trials, hence the designation artificially less active. During trial three, both large and small mice were attached to long tethers and permitted unrestrained movement across the trial board. This approach allowed us to investigate possible differences in the rate of movement between large and small mice, thus enabling us to determine which facet

of mouse activity (time of movement or rate of movement) appeared to be more important in eliciting a predatory response by hunting kestrels. Mice that were less active during these trials were designated normally less active.

Kestrels were located while driving through the study area which was primarily agricultural and ranch land dominated by pasture and hay fields. Upon spotting a perched kestrel, the automobile was gradually halted along the roadside or in an adjacent field. Trials began when the board was placed on the ground and the investigator stepped away. The trial board was generally placed 10–50 m (\bar{x} = 36.8 m, SD = 31.1, N = 147) from the automobile in a position allowing kestrels an unobstructed view of the mice. During each trial, mouse activity was observed from the automobile with 8× binoculars. Activity was documented by describing the behavior of each mouse into a portable cassette recorder. For the duration of the trial period, each mouse was assigned to one of two categories: moving (when a mouse crossed one or more squares on the trial board or moved within a 10-cm square), and not moving (when a mouse failed to cross or move within a square). Rate of movement was measured as the number of squares crossed/min. Kestrels were allowed 5 min to initiate an attack. To simulate natural conditions as much as possible, mice chosen by kestrels were automatically released from the board by pulling a string attached to the clothespin and subsequently carried away by the kestrel. If no response occurred within 5 min, the trial was terminated. All trials were terminated in which mice pulled vigorously at their tethers and were not included in the analysis (N = 5). Only the first attacks from all birds that were thought to be presented mice repeatedly were used in the analysis.

Chi-square goodness of fit (Zar 1974) was used to analyze prey choice by males and females. Differences in the activity between mice were analyzed by a Student's t -test on the arcsine transformation of the total trial time individuals were moving. The rate of movement of large and small mice was also analyzed by a Student's t -test. Due to small sample size for trial one, data for both sexes were combined.

RESULTS

Kestrels exhibited overwhelming selection for active (90% of choices) vs. inactive (dead) mice in trial one (χ^2 = 28.1, df = 1, P = 0.0001) (Table 1). For trial two (large mouse/long tether, normally more active vs. small mouse/short tether, artificially less active or vice versa) female (χ^2 = 12.7, df = 1, P = 0.0004, N = 38) and male kestrels (χ^2 = 11.3, df = 1, P = 0.0008, N = 39) selected normally active mice over artificially less active mice (Table 1). In trial three (small/large mouse long tether) females (χ^2 = 14.6, df = 1, P = 0.0001, N = 41) and males (χ^2 = 18.2, df = 1, P = 0.0001, N = 29) chose the normally more active mouse over the normally less active mouse and showed no selection for size (P > 0.05; Table 1). We found no evidence of differences

Table 1. Number of mice selected by American kestrels during field trials (NA = normally active, NLA = normally less active, ALA = artificially less active; see text for explanation).

TRIAL 1			
KESTREL SEX	MOUSE SIZE	ACTIVE	INACTIVE
Both	Large	18	0
	Small	13	1
	Total	31	1
TRIAL 2			
		ACTIVITY	
		NA	ALA
Female	Large	15	3
	Small	15	5
	Total	30	8
Male	Large	15	5
	Small	15	4
	Total	30	9
TRIAL 3			
		ACTIVITY	
		NA	NLA
Female	Large	18	4
	Small	15	4
	Total	33	8
Male	Large	12	2
	Small	14	1
	Total	26	3

in hunger state between the a.m. and p.m. as there was no selection for either size of mouse in the morning ($\chi^2 = 0.001$, $df = 1$, $P > 0.05$, $N = 64$) or afternoon ($\chi^2 = 0.016$, $df = 1$, $P = >0.05$, $N = 83$). In further support of this observation, no difference was detected in the number of failures to respond to mice between morning and afternoon ($\chi^2 = 0.002$, $df = 1$, $P > 0.05$, $N = 272$).

Differences in the mean percent of trial time spent moving by mice selected (\bar{x} moving time = 19.8, $SD = 20.8$) and not selected (\bar{x} moving time = 9.6, $SD = 12.7$) by kestrels were significant ($t = 4.99$, $df = 145$, $P = 0.0001$, $N = 147$). The rate of movement (or the speed that a mouse moved across the board) between large mice ($\bar{x} = 10.9$ squares/min, $SD = 11.4$) and small mice ($\bar{x} = 10.1$ squares/min, $SD = 10.0$), however, was not significantly different ($t = 1.47$, $df = 80$, $P = 0.44$, $N = 82$).

Upon being presented with mice, female and male kestrels exhibited no difference in the time that they waited to select a mouse. This trend was consistent throughout fall/winter (female \bar{x} time to select a mouse = 147.0 sec, $SD = 106.6$; male \bar{x} time to select a mouse = 136.9 sec, $SD = 96.7$; $t = 2.97$, $df = 69$, $P = 0.38$, $N = 71$), and spring/summer (female \bar{x} time to select a mouse = 146.4 sec, $SD = 111.8$, male \bar{x} time to select a mouse = 157.9 sec, $SD = 96.6$; $t = 0.93$, $df = 52$, $P = 0.46$, $N = 54$). Finally, the number of occasions that males and females failed to choose a mouse did not differ during the breeding season ($\chi^2 = 0.01$, $df = 1$, $P > 0.05$, $N = 74$), as well as during the rest of the year ($\chi^2 = 0.002$, $df = 1$, $P > 0.05$, $N = 198$).

DISCUSSION

Our results differ from previous field studies addressing kestrel prey selection (Drye 1980, Smallwood 1981, Bryan 1984). Although the mice used in our study were similar in size to the mice used in earlier studies, none of the previous studies quantified prey activity during trials in which mice were offered to kestrels. In a subsequent study Smallwood (1989) demonstrated significant selection by kestrels for moving mice over nonmoving (drugged) mice when each category of mouse was presented singly to kestrels. He also reported that kestrels selected large mice over small mice in paired presentations because large mice moved at a greater rate.

We, like Smallwood (1989) observed kestrels to select more active mice in all trials. Trial one (small or large inactive mouse versus small or large active mouse) demonstrated most convincingly kestrel selection for active over inactive prey; two mice were presented simultaneously, as opposed to a solitary mouse by Smallwood (1989). Although one could argue that kestrels probably do not commonly encounter two prey items simultaneously under natural conditions, our approach has merit because on occasion birds chose the inactive mouse over the active one. In addition, the mice used in our study did not exhibit size-dependent activity like the mice in Smallwood's (1989) study, which suggests that prey type (e.g., strain) could influence the outcome of studies investigating the role of prey activity in prey choice.

Similar amounts of time to select large and small mice along with an almost identical number of non-responses made by females and males, suggest that both sexes hunt with equal effort throughout the

year and that there appears to be no change in hunting strategy during the breeding season. This interpretation should be considered only within the scope of our experimental design and the population of birds that we were testing.

Although kestrels select more active over inactive or less-active prey, the visual mechanisms involved remain uncertain. Smallwood (1989) speculated that prey characteristics along with size-dependent movement work in concert to elicit an attack, but subsequently added that prey activity is ultimately more important than prey size. This response to prey movement is most likely influenced by the various features of the falconiform eye which appear to be adaptations for improving detection of movement (Hirsch 1982). Within the range of prey sizes used in this study, however, prey size appears to be of little or no consequence in prey choice decisions, and we suggest that if prey size and activity work in concert to elicit an attack, the effect is slight. Future research would benefit from presenting paired mice of equal size that would test selection for active prey without the possible confounding influence of size.

In summary, this study showed that within the range of prey sizes available, kestrels chose prey on the basis of activity, and exhibited little size discrimination in prey choice decisions. Males and females also did not exhibit differences in hunting strategies, at least as we defined them, during different seasons of the year.

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SPRING 1994 RAPTOR MIGRATION AT EILAT, ISRAEL

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ABSTRACT.—In the Old World, most raptors and other soaring birds breed north of 35°N latitude and winter between 30°N and 30°S. An estimated 3 000 000 raptors from Europe and Asia migrate through the Middle East. Israel is the only land bridge for birds migrating south between Europe and Asia to Africa in autumn, and north to their breeding grounds in spring. In spring 1994 a total of 1 031 387 soaring birds were counted in 92 d of observation. Of these 1 022 098 were raptors of 30 species, for an average of 11 110 raptors per day. The most abundant species were the honey buzzard (*Pernis apivorus*) and the steppe buzzard (*Buteo buteo vulpinus*). Levant sparrowhawks (*Accipiter brevipes*), steppe eagles (*Aquila nipalensis*), and black kites (*Milvus migrans*) numbers were smaller by an order of magnitude. A total of 1999 raptors were unidentified to species (0.19% of total).

KEY WORDS: *Eilat; Israel; migration; raptors; spring 1994; survey.*

Migración de rapaces en la primavera de 1994 en Eilat, Israel

RESUMEN.—En el viejo mundo, la mayoría de las rapaces y otras aves planeadoras nidifican al norte de los 35°N, y en invierno se encuentran entre los 30°N y 30°S. Se ha estimado en tres millones de rapaces de Europa y Asia que migran a través del Medio Este. Israel es solamente el puente de tierra para aves que migran a África desde Europa y Asia durante el otoño, y al norte durante la primavera hacia sus áreas reproductivas. En la primavera de 1994 un total de 1 031 387 de aves fueron contadas en 92 días de observación. De ellas, 1 022 098 fueron rapaces de 30 especies, i.e., con un promedio de 11 110 rapaces por día. Las especies más abundantes son *Pernis apivorus* y *Buteo buteo vulpinus*. *Accipiter brevipes*, *Aquila nipalensis* y *Milvus migrans* resultaron ser menos abundantes en un orden de magnitud. Un total de 1999 rapaces no fueron identificados a nivel de especies (0.19% del total).

[Traducción de Ivan Lazo]

Since Christensen et al. (1981) published their classic report on the phenomenon of a bottleneck of raptors and other soaring birds over the northern tip of the eastern arm of the Red Sea, several raptor migration (Thomson 1953) surveys have been made in spring and autumn (Shirihai 1987, 1988, Shirihai and Yekutieli 1991, Shirihai and Christie 1992). The most recent survey was in the spring of 1988.

In the Old World, most raptors breed north of 35°N latitude and winter between 30°N and 30°S (Shirihai and Christie 1992). An estimated 3 000 000 raptors from Europe and Asia migrate through the Middle East. The largest count achieved in a survey was in 1985 wherein 1 193 229 raptors of 27 species (Shirihai and Christie 1992) were counted in 100 days (for method see Thomson 1953).

Eilat is at the hub of the only land bridge between three continents, and is a junction for birds migrating south between Europe and Asia to Africa in autumn and north to their breeding grounds in spring (Safriel 1968, Yom-Tov 1988). Almost 300 bird species mi-

grate over this southern point of Israel including waders, waterfowl, passerines, and pelagic species. These latter species are mostly nocturnal migrants (Bruderer 1994).

Eilat is at the southern end of the Arava Valley which forms part of the rift valley, a tectonic depression extending from Anatolia to central Africa (Safriel 1968). On the Israeli side of the valley (west) the mountains reach heights of 700 m above sea level, and on the Jordanian side (east) about 1200 m.

Eilat is on the northern fringe of the Saharo-Arabian desert belt at the edge of almost 2000 km of continuous desert. Additionally, to the north-northeast are 650 km of the Syrian Desert, and the Arabian Desert lies to the east (Fig. 1). Hence many birds land in Eilat to rest before (in autumn) or after (in spring) crossing these deserts (Yom-Tov 1988). The northward journey of those that have overwintered in Africa is directed north or northeast in the shortest route to their Palearctic or Holarctic breeding grounds.

Until recently it was assumed that the rift valley was a convenient flyway that funneled the migrants headed north from eastern Africa (Yom-Tov 1988). However, detailed studies (e.g., Safriel 1968, Wimpfheimer et al. 1983, Shirihi and Christie 1992), suggest that the routes bypass the Red Sea, cut across the Sinai Peninsula, and converge over the northern part of its eastern arm, at Eilat or slightly further north. A proportion of migrating birds also cuts across the Straits of Jubal toward Ras Muhammad and Sharm-el-Sheikh (Christensen et al. 1981). These birds then continue north along the cliffs of the Gulf of Aqaba coastline. This explains why large concentrations of soaring birds are seen mostly in the spring (February to May) at Eilat in the diurnal hours (Yom-Tov 1988), and why migrating waders, waterfowl, passerines (Bruderer 1994) and raptors (Stark and Liechti 1993) can be detected by radar at night.

METHODS

Observations were made at three points for approximately 12 h a day from 15 February to 19 May 1994, except for 2 d of sandstorms; 92 d of observations were carried out. Each raptor observation included the exact time of observation, species, exact or estimated number seen, estimated height and direction of flight, and prevailing weather conditions. Counting of small flocks (up to mid-hundreds) was fairly accurate by counting individual birds or groups of ten; and flocks of thousands were counted to within an accuracy estimated as $\pm 10\%$ or better (similar to Shirihi and Christie 1992). Double counts were eliminated by comparing recording sheets at the end of the day. All data were summarized by 5-d periods for all species, and compared to previous surveys.

Observation points were close to those used by Christensen et al. (1981) and were improved by Hadoram Shirihi (Shirihi and Christie 1992). The observation points were such that soaring birds frequently flew within 50 m of the observers in mornings and late evenings. During midday the birds used thermals and could be discerned only with binoculars or telescopes. The use of telescopes considerably increased the number of identified individuals. The extensive information provided by previous surveys allowed us to concentrate on the best areas at the best times of the day. However, observers were at all stations at all times, even if no birds were expected in the vicinity.

I classified the species according to the scheme suggested by Shirihi and Christie (1992), who separated the species into four classes based on their relative abundance in migration at Eilat. The most abundant species were further subdivided into two levels: level 1 were those seen in hundreds of thousands and level 2 in tens of thousands. Common species were in their hundreds, uncommon species in tens, and rare were singles. This scheme was chosen for consistency because Shirihi and Christie (1992) analyzed the migration of six (nonconsecutive) springs, and my study represents only spring 1994.

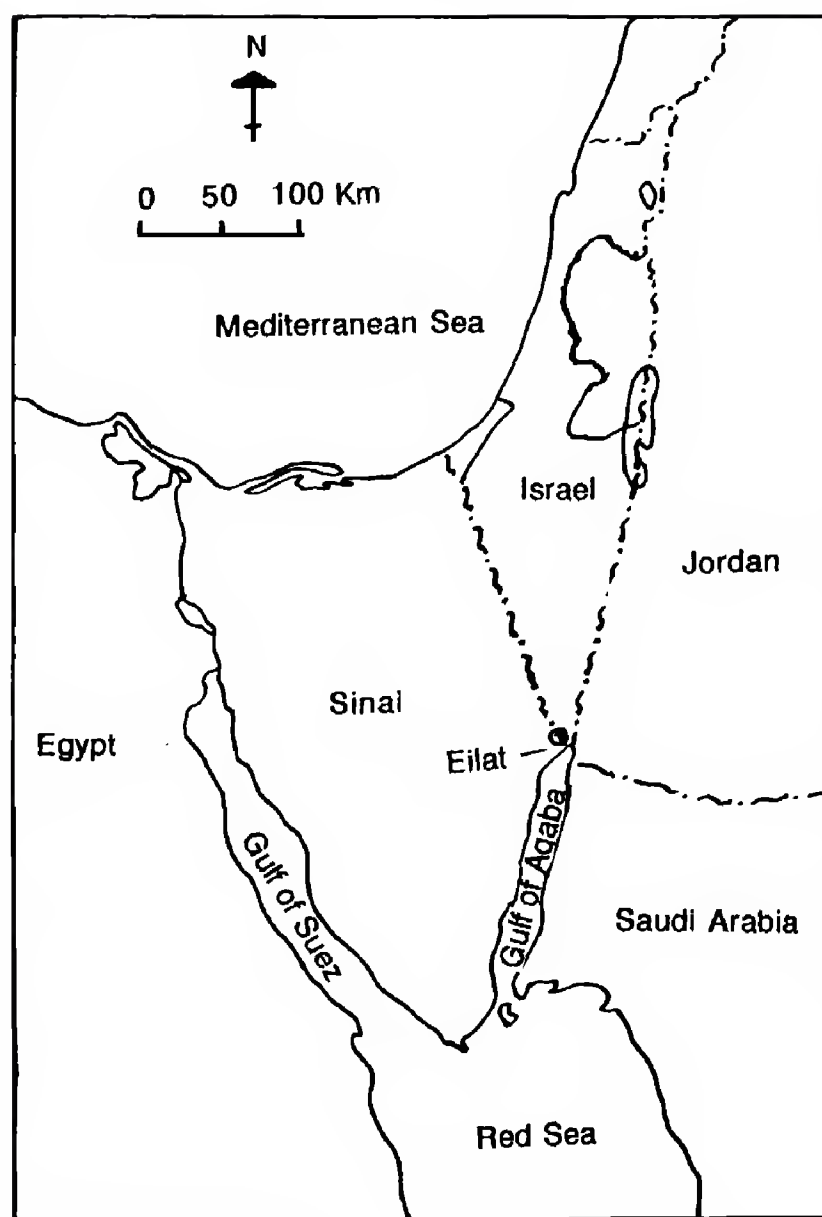


Figure 1. Map of the region showing location of Eilat. Curved line with dots represents international boundaries

RESULTS

A total of 1022098 raptors of 30 species were counted in 92 d of observation (Table 1); i.e., an average of 11110 raptors per day. The most abundant species in my survey were the honey buzzard (*Pernis apivorus*) and steppe buzzard (*Buteo buteo vulpinus*; Table 1). Levant sparrowhawks (*Accipiter brevipes*), steppe eagles (*Aquila nipalensis*; see Clark 1992) and black kites (*Milvus migrans*) numbers were smaller by an order of magnitude. Egyptian vultures (*Neophron percnopterus*), short-toed eagles (*Circus aeruginosus*), booted eagles (*Hieraaetus pennatus*), osprey (*Pandion haliaetus*), marsh harriers (*Circus aeruginosus*), and sparrowhawks (*Accipiter nisus*) were seen in hundreds. Griffon vultures (*Gyps fulvus*), Bonelli's eagles (*Hieraaetus fasciatus*), long-legged buzzards (*Buteo rufinus*), pallid harriers (*Circus macrourus*), lesser kestrels (*Falco naumanni*), Eurasian

kestrels (*Falco tinnunculus*), hobbies (*Falco subbuteo*), and Eleonora's falcons (*Falco eleonorae*) were uncommon species.

A total of 1999 raptors were unidentified (0.19% of total). Of these the majority (1685, 0.16%) were due to uncertainty of identification between species with similar flight or silhouette, or were observed from a distance that did not allow a good view. In this category, 1557 (0.15%) remain unclassified as steppe/honey buzzards, 104 (0.01%) as lesser/Eurasian kestrels, and 24 (0.002%) as sparrowhawks. In addition, others identified to genus were 37 harriers (*Circus* spp.), 29 eagles (*Aquila* spp.), and 21 medium to large falcons (*Falco* spp.). Only 227 (0.02%) raptors could not be further classified.

Abundant Species. Level 1. The honey buzzard was a very late migrant and the most numerous (Fig. 2). It comprised 52% of the total spring migration. The first individuals were seen on 17 April and peak migration was between 1–5 May (51% of total seen). The largest number seen in a single day was on 2 May when 176 424 honey buzzards were counted. Small flocks were still passing at the termination of the survey and migration of this species in mid-June has been previously documented (Shirihai and Christie 1992).

The steppe buzzard was the second most numerous species and comprised 36% of the total migration. Observed regularly throughout the season, peak migration was on 28 March when 39 832 recorded (Fig. 2). Our observations concur with Clark et al. (1986) and Gorney and Yom-Tov (1994) that most, if not all, buzzards observed belong to the eastern subspecies *B. buteo vulpinus*.

Level 2. Levant sparrowhawks constituted 4.2% of the total migration. This confirmed the numbers (40 000–50 000) seen on migration in previous years in autumn (Dovrat 1991) or spring (Shirihai and Christie 1992). Recent radar studies (Stark and Liechti 1993) indicate that visual censuses may be deficient for this species because it is possible that a part of the population migrates at night. The numbers observed in migration are greatly in excess of those reported from the breeding range (V.M. Galushin pers. comm.) and warrants further study to locate unidentified regions where this species breeds, or to determine if a significant population of non-breeders comprises the population seen in migration. Shirihai and Christie (1992) report that in previous surveys the earliest Levant sparrowhawk seen was on 25 March. In the present study the first was seen

on 19 March and the last on 5 May (Fig. 2). Peak migration occurred over 2 d when compact flocks of thousands were observed. On 25 April 25 522 were seen and on 26 April an additional 14 472; i.e., 90% of the observations occurred within a span of 48 hr. This concurs with earlier reports (Phillips 1915, Hollom 1959, Safriel 1968, Shirihai and Christie 1992) that peak migration of this species occurs on 25 or 26 April (Shirihai and Yekutieli 1991).

Steppe eagles formed 3.0% of total raptors seen. My data concur with those of Safriel (1968) and Shirihai and Christie (1992) that the steppe eagle migration begins in late January with a major peak occurring between the third week of February and mid-March and a smaller secondary wave in mid-April (Fig. 2). On 4 March the largest number (4292) was counted. Considered to be a species that is observed in small numbers throughout spring, the last individual was observed on 9 May. It constituted 99.5% of all *Aquila* eagles seen.

Black kites were the only species counted in considerably lower numbers in the 1994 survey compared to previous studies. The 15 659 kites seen is well below the minimum of 24 728 seen in 1986. In the 1994 survey, they comprised only 1.5% of total raptors observed in comparison to 2–4.6% in previous years. Peak migration, when 1000–2000 kites per day were seen, was spread over 2 wk—22 March to 2 April. Although seen throughout late April and May, appearance was irregular with many days having no kites at all.

Common Species. The Egyptian vulture comprised 0.04% (417) of the total raptors observed, and was within the range of previous surveys (263–802). Present in small numbers throughout the survey period, these vultures had the same three peak migration periods (>30 per day) described by Shirihai and Christie (1992).

The short-toed eagle was seen from mid-February until late April and peak migration (10 per day) was spread from 12–31 March. In spring, the species migrated mostly in pairs and mingled with other species in thermals.

Sparrowhawks are solitary migrants and their size and flight at low altitudes makes it difficult to spot and identify them. So, more may migrate through Eilat than the 122 seen. However, their relative abundance in the migration could possibly represent their peak migration period. The maximum numbers (>3 per day) were seen between 6 and 25 April.

The first marsh harrier was seen on 11 March

Table 1. Number of raptors counted at Eilat, Israel, Spring 1994. Question mark denotes species not officially accepted to occur in the region.

SPECIES	1994 SPRING SURVEY	MEAN ANNUAL SPRING SURVEY (1977–88) ^a	RANGE FOR ALL SPECIES
Total all raptors	1 022 098	795 228	474 124–1 193 229
Honey buzzard (<i>Pernis apivorus</i>)	545 562	363 221	188 914–851 598
Black kite (<i>Milvus migrans</i>)	15 735	28 249	24 728–31 774
White-tailed eagle (<i>Haliaeetus albicilla</i>)	0	0	0–2
Pallas’s fish eagle (?) (<i>Haliaeetus leucoryphus</i>)	1	0	0
Egyptian vulture (<i>Neophron percnopterus</i>)	417	428	263–802
Griffon vulture (<i>Gyps fulvus</i>)	14	10	2–22
Cinereous vulture (<i>Aegypius monachus</i>)	0	0	0–1
Short-toed eagle (<i>Circaetus gallicus</i>)	159	162	59–345
Bateleur (<i>Terathopius ecaudatus</i>)	0	0	0–1
Marsh harrier (<i>Circus aeruginosus</i>)	120	179	71–371
Hen harrier (<i>Circus cyaneus</i>)	0	0	0–1
Pallid harrier (<i>Circus macrourus</i>)	57	57	7–113
Montagu’s harrier (<i>Circus pygargus</i>)	7	19	7–55
<i>Circus</i> spp.	37	28	1–3
Goshawk (<i>Accipiter gentilis</i>)	0	1	1–3
Sparrowhawk (<i>Accipiter nisus</i>)	122	163	52–456
Shikra (<i>Accipiter badius</i>)	0	0	0–1
Levant sparrowhawk <i>Accipiter</i> spp.	44 524 24	16 281 298	905–49 836 0–1360
Steppe buzzard (<i>Buteo buteo vulpinus</i>)	381 516	326 278	142 793–465 827
Long-legged buzzard (<i>Buteo rufinus</i>)	65	45	28–105
<i>Pernis/Buteo</i> spp.	1557	41 260	3757–149 258
Lesser spotted eagle (<i>Aquila pomarina</i>)	65	54	21–74
Spotted eagle (<i>Aquila clanga</i>)	2	6	4–10
Steppe eagle (<i>Aquila nipalensis</i>)	31 198	28 032	10 922–75 053

Table 1. Continued.

SPECIES	1994 SPRING SURVEY	MEAN ANNUAL SPRING SURVEY (1977–88) ^a	RANGE FOR ALL SPECIES
Imperial eagle (<i>Aquila heliaca</i>)	52	47	12–95
Golden eagle (<i>Aquila chrysaetos</i>)	10	1	0–7
<i>Aquila</i> spp.	29	2560	17–9083
Booted Eagle (<i>Hieraaetus pennatus</i>)	140	138	105–175
Bonelli's eagle (<i>Hieraaetus fasciatus</i>)	12	3	0–6
Osprey (<i>Pandion haliaetus</i>)	101	83	49–130
Lesser kestrel (<i>Falco naumanni</i>)	83	22	0–55
Eurasian kestrel (<i>Falco tinnunculus</i>)	80	57	11–190
Red-footed falcon (<i>Falco vespertinus</i>)	6	2	0–12
Merlin (<i>Falco columbarius</i>)	0	0	0–1
Hobby (<i>Falco subbuteo</i>)	22	23	6–54
Eleonora's falcon (<i>Falco eleonora</i>)	17	10	6–21
Sooty falcon (<i>Falco concolor</i>)	5	1	0–2
Lanner (<i>Falco biarmicus</i>)	0	3	0–7
Saker (<i>Falco cherrug</i>)	0	0	0–2
Peregrine falcon (<i>Falco peregrinus</i>)	4	1	0–4
Barbary falcon (<i>Falco pelegrinoides</i>)	3	1	0–3
<i>Falco</i> spp.	125	28	0–68
Unidentified raptors	227	1824	0–8601

^a Shirihi and Christie (1992).

and the species was present in small numbers throughout the survey. Two peaks were evident between 22 March to 10 April and 21–27 April when up to five marsh harriers were observed per day.

Uncommon Species. Imperial eagles were seen throughout the survey. Although two main periods of migration have been previously described (Christensen et al. 1981, Shirihi and Christie 1992) that pattern was not evident in 1994.

Although the lesser spotted eagle was regularly seen in small numbers from mid-March to mid-

April, the first was seen on 22 February. It is possible that some individuals of this species were misidentified and counted as steppe eagles, especially when seen from a distance.

Booted eagles are dispersed and solitary migrants. Eighty-nine percent of the 130 seen occurred between 22 March and 20 April. Of the two morphs known for this species, 53% seen at Eilat were the light morph and 47% the dark (for descriptions see Holmgren 1984, Clark 1987). This ratio is consistent with previous studies (e.g., Christensen et al.

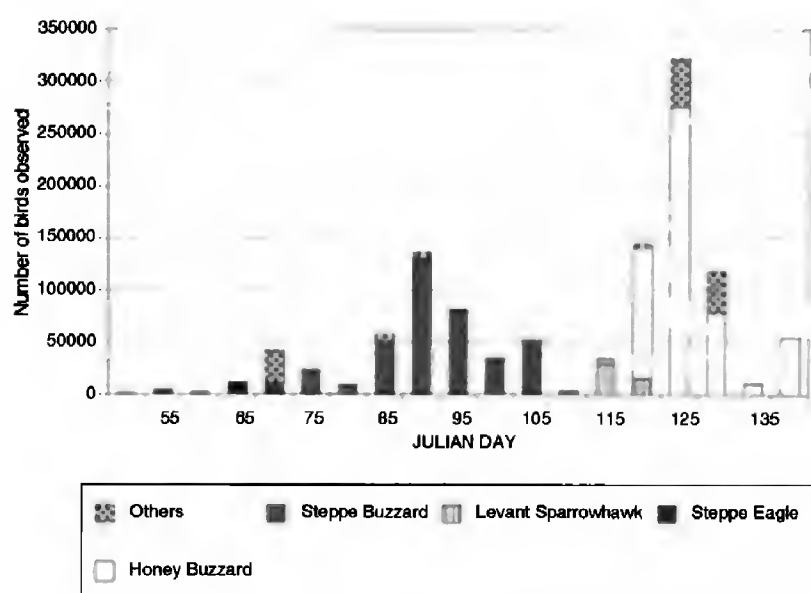


Fig. 2. Phenology of the four dominant species of raptors in spring migration at Eilat, Israel. Data are presented in 5-d periods. These four species comprise 65–98% of the raptors seen during any given period.

1981, Shirihai and Christie 1992) and is attributed to the fact that dark-morph booted eagles are easily overlooked when they are part of black kite flocks. Christensen et al. (1981) assumed that the two morphs comprise a 50:50 ratio in the natural population.

The osprey is considered a rather scarce migrant and was regularly observed from 19 March until 8 May, during which at least one bird per day was seen. The largest number occurred on 24 March when 10 were observed. Ospreys are mostly solitary migrants, but they can occasionally be observed in thermals with small flocks. Although there are no breeding pairs in the immediate area, an individual that loitered at the shore was excluded from all counts.

Long-legged buzzards migrate in small numbers from late-February to late-April. Numbers may have been underestimated because of its similarity to and tendency to migrate with the more common steppe buzzard (see Shirihai and Forsman 1992).

Pallid harriers were seen only for 3 wk—between 19 March and 11 April. Peak migration was on 23 March when 14 individuals were recorded. Gender difference in timing of migration was obvious. Males migrated from 19 March until 3 April, and females from 29 March until 11 April. Similar to the report of Shirihai and Christie (1992), no juveniles were seen in 1994.

Montagu's harriers (*Circus pygargus*) migrated about a week later than pallid harriers, i.e., from 8 to 23 April. Although classified as an uncommon

species, only seven were seen during the survey period. They are more commonly seen along valley floors, e.g., 33 km north of Eilat.

Solitary hobbies were seen in small numbers from 17 April and on throughout the survey. Some may have been missed owing to their low, dodging flight in the canyons below the observation posts.

Allowing for the local breeding population of Eurasian kestrels, only birds that displayed migratory behavior (e.g., no hunting, no loitering) were included in final tally. They were observed in small numbers throughout the survey.

Rare Species. A Pallas's fish eagle (*Haliaeetus leucorhynchus*) sighting is the first for the region and the observation remains unconfirmed. The crested honey buzzard (*Pernis ptilorhynchus*), also a first for the region, was observed by Hadoram Shirihai on Mount Yishay in early May, but not by any observers in my survey.

Most (9 of 14) griffon vultures were recorded early in the survey—between 21 February and 4 March. They were always seen in flocks of steppe eagles and/or black kites.

Spotted eagles were only seen in late February. Possibly some were misidentified when flying in thermals with lesser spotted or steppe eagles. Migrating Bonelli's eagles were rare sightings.

The lesser kestrel was a rare but regular migrant. The peak of 67 (81% of total for survey) occurred on 19 March, but it is possible that many were missed because it migrates mostly along coasts and in open areas. Ninety-one unidentified kestrel species could have included lesser kestrels. Red-footed falcons (*Falco vespertinus*) were rare migrants and although known to migrate gregariously on other routes, were always observed singly at Eilat. The species was seen between 7 April and 5 May. Eleonora's falcon (*Falco eleonora*) was a late migrant, solitary, and occurred in small numbers. Observed between 15 April and 7 May, single birds were reported until late June. The sooty falcon (*Falco concolor*) was also a late migrant, solitary, and occurred in very low numbers. Shirihai and Christie (1992) considered the ones seen in Eilat to be those that breed in the Dead Sea or Negev Desert regions. Peregrine falcons (*Falco peregrinus*) were rare, sporadic, and seen singly. The first one was seen 22 February, the second on 23 March, and two more on 24 and 25 April, respectively. Allowing for the local breeding population of about two pairs, only barbary falcons (*Falco pelegrinoides*) that displayed migratory behavior were

included in final tally. These falcons were seen singly on 17, 24, and 27 April.

DISCUSSION

Migration was dominated in the eastern Palearctic by two species, honey buzzard and steppe buzzard (Table 1). At Eilat the three dominant species comprised between 65–98% of the birds seen on any given day (Fig. 2). Most flocks were mixed-species flocks with black kite, steppe eagle, imperial eagle (*Aquila heliaca*), lesser spotted eagle (*Aquila pomarina*), short-toed eagle, and Egyptian vulture being the species most often observed with honey buzzards and steppe buzzards. On the other hand, harriers and falcons were almost always seen singly.

Political instability in the Middle East and in other areas (e.g., former Yugoslavia) that lie in the path of major migratory routes make it especially important to periodically monitor avian populations. Monitoring migrating raptors is one of the most reliable methods of evaluating their populations. Other techniques such as banding (e.g., Clark et al. 1986), understanding parameters influencing flight-distance capabilities and physiological constraints (e.g., Gorney and Yom-Tov 1994), and evaluation of blood parasites as markers of the movements of bird populations (e.g., Earle 1993) should also be undertaken.

The variation in raptor migration among years at Eilat indicates that results obtained there should be used cautiously in representing population trends on a species level. Very few species have data that might be reliably used for that purpose (e.g., Levant sparrowhawk). Most other species are known to use alternative routes if inclement weather prevails (e.g., steppe eagles, steppe buzzards). The very low numbers of black kites observed during this survey may, for example, be explained if the majority of the population followed routes further north of Eilat. Annual and seasonal surveys conducted at regular intervals would allow the evaluation of future trends. The present political stability in the region may allow ornithologists to conduct simultaneous surveys at the other well-known bottlenecks. Only comprehensive and coordinated surveys will aid in evaluating the existing populations of raptors in the Palearctic, and the respective proportions that follow the various routes through the Middle East.

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SHORT COMMUNICATIONS

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AMERICAN KESTREL REPRODUCTION AND DISPERSAL IN CENTRAL WISCONSIN

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KEY WORDS: *American kestrel; Falco sparverius; natal dispersal; nest box; reoccupancy; reproduction.*

Short-term studies (≤ 3 yr) on avian population dynamics are likely to produce incomplete or incorrect perceptions (Wiens 1984). During a 13-yr study I examined long-term (≥ 10 yr) productivity and natal dispersal (movement between birth place and breeding site [Greenwood 1980]) of American kestrels (*Falco sparverius*).

STUDY AREA AND METHODS

Data were collected from a 75-km² area near Stevens Point in Portage County, Wisconsin (44°27'N, 89°40'W), with elevations ranging from 330–363 m above sea level. This area consisted of farmland interspersed with small woodlots, grasslands, and marshes.

During March 1979, nest boxes were placed 5–10 m above ground in small groups of trees (< 10 trees) near large clearings (> 250 ha). Nest boxes were constructed from 2.5-cm-thick rough-cut pine and followed Jacobs (1981) in design. Inside measurements were 25 × 20 × 47 cm (depth × width × height). The entrance hole was 7.6 cm in diameter and located 3.8 cm below the top of the front panel. The number of nest boxes available during the 13-yr study varied annually between 12–29 depending on placement of additional boxes and repair of damaged boxes. Gray squirrels (*Sciurus carolinensis*) and fox squirrels (*S. niger*) filled some of the nest boxes with nesting material, rendering them unusable for kestrels. From 1980 through 1991, old nesting material was replaced with fresh bedding of wood chips in March.

Nest boxes were inspected during mid-June to determine occupancy, and young were marked with U.S. Fish and Wildlife Service bands. I considered a nest box to be occupied if evidence of nesting was present (eggs, eggshells, or young). Due to time constraints, I was unable to monitor each nest box throughout the entire nesting season. Some nest failures may have been missed during incubation or after banding. To account for this I applied the Mayfield Model (Mayfield 1961) to my data for an estimate of the overall success rate of nests. This method is based on nest failures in relation to days of coverage. A nest box was considered successful if at least one young reached a bandable age (16–28 d). I used the number of young banded per successful nest as an index to the fledging rate (Henny

1972). A nest box was considered reoccupied if it was occupied by kestrels in two or more successive years. An unknown number of kestrels fledged from 14 nest boxes prior to banding and were not included in the fledging rate index.

Natal dispersal distances were determined from kestrels banded as nestlings and encountered during a subsequent breeding season (April to July). Dispersal distances were measured from the hatching site to the encounter site as reported by the U.S. Fish and Wildlife Service Bird Banding Laboratory.

RESULTS

Of 262 nest boxes available for use in all years combined, 183 (70%) were occupied by kestrels. Overall, 70% of the occupied boxes were estimated to be successful (Mayfield Model). Of the 42 nests where the Mayfield Model could be applied, 37 were successful. Using the conventional method this would have been reported as a success rate of 88% (37/42). When the Mayfield Model was applied to the same data the success rate decreased to 70%. Reproduction was stable during this study. Mean brood size each year in successful nests varied but not significantly ($P > 0.05$) from the 13-yr mean of 4.1 young (Table 1). Of the 172 boxes available for ≥ 2 consecutive years, 116 (67%) were reoccupied the next year.

Nine of 603 (1.5%) young that I banded were encountered in a subsequent breeding season. A female banded as a nestling in another population was captured as a breeder in my study area and was included in the natal dispersal distances (J. Jacobs pers. comm.). Five of these kestrels were captured at nest boxes as breeders, and five were reported dead during the breeding season and assumed to be breeders (Table 2.). The median dispersal distance for females ($N = 7$) was 30 km and 16 km for males ($N = 3$). Seven of the 10 kestrels were encountered within 35 km of their natal area.

DISCUSSION

American kestrels readily accepted the nest boxes even when natural cavities were available (see also Hamerstrom et al. 1973, Jacobs 1981, Toland and Elder 1987). I did not determine what impact, if any, the nest boxes had on kestrel densities. The occupancy rate (70%) of nest boxes by American kestrels in central Wisconsin was identical

Table 1. Nest box use and brood size of American kestrels in central Wisconsin (1979–91).

	YEAR											
	79	80	81	82	83	84	85	86	87	88	89	TOTAL
Number of boxes available	26	29	23	12	16	19	23	19	23	18	19	262
Percent occupied	62	79	74	75	56	47	61	63	87	83	84	70
Percent reoccupied ^a	—	88	74	47	56	56	56	71	92	50	87	67
Brood size per successful nest	4.0	4.2	4.5	3.2	3.6	4.6	4.5	4.1	3.7	4.6	3.7	4.1

^a Boxes occupied two years in succession.

Table 2. Natal dispersal distances and direction of Wisconsin kestrels.

SEX	YEAR FLEDGED	YEAR EN-COUNT-ERED	DISTANCE (km) AND DIRECTION		STATUS
			MOVED ^a		
Female	1979	1980	161	W	Breeder
Male	1980	1982	16	NW	Found dead
Male	1980	1982	362	SE	Found dead
Female	1982	1988	30	SE	Breeder
Female	1983	1987	2	SE	Breeder
Female	1986	1987	85	SE	Found dead
Female	1987	1988	19	SE	Breeder
Female	1987	1990	32	SE	Breeder
Female	1988	1989	30	W	Found dead
Male	1991	1992	4	NE	Found dead

^a From hatching site to nesting area.

to that found in Missouri (Toland and Elder 1987) and similar to the 73% rate found in Colorado (Stahlecker and Griese 1979). In California, Bloom and Hawks (1983) reported only 31% of their kestrel boxes were occupied. To estimate the recruitment standard for kestrels, Henny (1972) calculated an annual mortality rate of 69% for yearlings and 47% for adults from band returns. He assumed that 82% of the yearlings and all the adults attempted to breed. Based on these assumptions, Henny believed with 73% of the nests successful, each breeding female must produce 3.92 young per successful nest for the population size to remain constant. Seventy-seven percent of the band recovery data used to determine the recruitment standard came from northeastern United States, including Wisconsin. My average of 4.1 young per successful nest with 70% of the nests successful is similar to Henny's recruitment rate of 3.92. My results do not account for renest attempts and are probably a conservative estimate of actual productivity for each breeding female. These long-term data suggest the kestrel population was stable on my study area.

Although few, natal dispersal distances I present suggest that females dispersed farther than males. This is similar to peregrine falcons (*Falco peregrinus*; Ambrose and Riddle 1988), Cooper's hawks (*Accipiter cooperii*; Rosenfield and Bielefeldt 1992), and birds in general (Greenwood 1980). Seven of the 10 Wisconsin kestrels were encountered within 35 km of their hatching site. From a larger study Newton (1979) found 76% ($N = 201$) of sparrowhawks (*Accipiter nisus*) bred within 20 km of their natal area.

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Inc., and other landowners allowed placement of nest boxes on their properties.

RESUMEN.—Un estudio de 13 años (1979–91), sobre *Falco sparverius* nidificando en cajas anideras, promedió 4.13 juveniles marcados por nido exitoso; con un 70% estimado de cajas anideras exitosas. El número de juveniles por nido exitoso varió entre años pero no significativamente del promedio de 13 años. El 67% de las cajas anideras fue reocupado en dos o más años sucesivos. La mediana de la distancia de dispersión para hembras ($N = 7$) fue de 30 km y 16 km para machos ($N = 3$).

[Traducción de Ivan Lazo]

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SEX-SPECIFIC DIET ANALYSIS OF THE TAWNY OWL (*Strix aluco*) IN NORWAY

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KEY WORDS: Norway; sex-specific diet; *Strix aluco*; tawny owl

The diet of the tawny owl (*Strix aluco*) is well-known and, based on pellet analysis, shows broad variation (Mikola 1983). However, some aspects like the invertebrate

content (Cramp 1985) and sexual differences in prey choice (Bildstein 1992) are not expressed by pellet analysis. Digestion hampers identification of invertebrate species eaten, and makes it impossible to estimate the proportion of invertebrates present (e.g., Kirk 1992). A possible difference in diet between the sexes might arise from a mech-

anism advanced to explain reversed sexual dimorphism (RSD) in raptors (Andersson and Norberg 1981, Lundberg 1986). Females may reduce competition for food with males by taking larger prey than their smaller mates (e.g., Earhart and Johnson 1970); tawny owl females weigh 26% more than males on average (Hirons et al. 1984). However, this is difficult to verify by pellet examination since it is impossible to distinguish between pellets from males and females.

Stomach analysis may be a way to answer these questions provided that prey remains are intact (Hagen 1952, Cramp 1985). Our objectives were (1) to evaluate sexual differences in tawny owl diet, and (2) to quantify the invertebrate prey in the tawny owl diet.

METHODS

During 1987–93, 215 tawny owls, mainly killed in road accidents, were collected in southern Norway. The date of the find was recorded, the sex was determined by inspecting sex organs, and stomach contents were investigated. In 39% (39 males and 45 females), stomachs were empty. The remaining 61% (39 males and 93 females) contained at least one prey item. Reference collections were used to identify the prey remains. Vertebrates were counted directly when intact, or by using skulls and dentaries of mammals and skulls and mandibles of birds. Likewise, invertebrates were counted when intact, but occasionally by compiling remains if partially digested. The biomass of vertebrates was calculated by multiplying the respective average individual weight given in the literature by the number of individuals recorded for each species. The biomass of the invertebrates was mainly calculated by totaling the individual weights of prey items weighed, but values given in the literature were sometimes used.

Prey items were sorted into categories of increasing body weight. Because many (up to 18) invertebrates were present in a single stomach, only their occurrence in each stomach was counted in the numeric distribution (all were represented in the biomass distribution). For testing the numeric size distribution of prey, the Mann-Whitney *U*-test was used, except when testing male versus female diet where a chi-square test was the most appropriate. To compare our results with previous studies of tawny owl diets, the importance of prey species is expressed in two ways: (1) the percentage biomass of each species among all species recorded, and (2) the numerical occurrence of prey species.

RESULTS

A higher proportion of females than males contained prey in their stomachs ($\chi^2 = 5.63$, $P < 0.05$). Invertebrates comprised 2.7% of the total biomass and 41.6% of the prey by number (Table 1). Lepidoptera, mostly *Noctua pronuba* larvae, dominated both by biomass (2.5%) and numerically (37.2%). Stomachs of females in particular were filled with Lepidoptera, although no significant difference was found between males and females overall (Mann-Whitney *U* = 21.5, $P > 0.05$).

The distribution of different size prey differed significantly between males and females ($\chi^2 = 10.83$, $P < 0.05$).

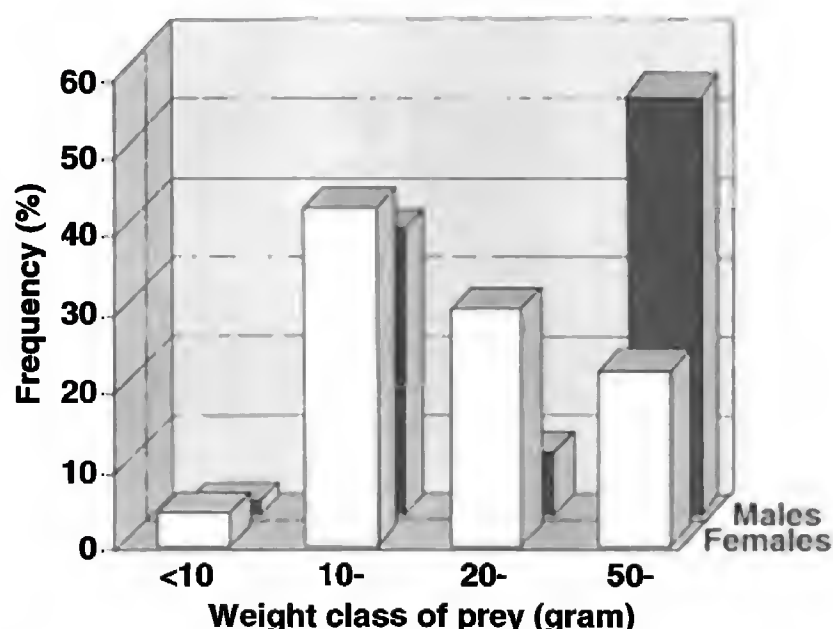


Figure 1. Prey mass distribution in the diet of Norwegian tawny owls.

Females diets' were over-represented with 20–30 g animals such as the field vole (*Microtus agrestis*), but males took more of the heaviest items (Norway rat, *Rattus norvegicus*, and birds). In regard to biomass distribution, 49% of the prey of males were in the heaviest prey group, although many prey were small- to medium-sized, with another peak (33%) at 15–19 g (Fig. 1). Females obtained 64% of their prey by weight from intermediate items (15–29 g), with a minor secondary peak in the heaviest prey (16%). Overall, small mammals predominated while birds accounted for approximately one-third of the diet biomass.

DISCUSSION

Previous studies lacked complete calculation of the biomass of invertebrates. Compared with 2.7% in our study, Labes (1990) found Coleoptera to be represented by <0.3% and Galeotii et al. (1991) reported Arthropods constituting 0.5% of tawny owl prey biomass. Most of the invertebrates in our specimens were identified as larvae of *Noctua pronuba*, which may occur in large numbers in southern Norway (Skou 1991). Even though invertebrates represented a small part of the total prey biomass, the stomachs of 27.3% of owls that had preyed upon larvae contained six or more items (range 6–19), thus perhaps indicating the periodic importance of this prey.

Southern (1968) found that 57% of 239 invertebrates recorded were beetles (*Carabus*) and 29% earthworms (*Lumbricus terrestris*). We found that 42% of the total prey ($N = 269$) in our study were invertebrates, differing little from Southern's results. However, small mammals and birds predominated as prey of Norwegian tawny owls, and males more than females preyed upon the heaviest items.

According to Snyder and Wiley (1976), the degree of RSD in a species shows a strong relationship with the proportional occurrence of birds in the diet. Two other trends correlate with a high degree of RSD—the prey is increasingly active and agile (Newton 1979) and larger relative to the predators (von Schantz and Nilsson 1981). Both these relationships mean that smaller body size will be favored since the prey requires more search and pursuit

Table 1. Prey items ($N = 269$) from stomach analyses of 131 Norwegian tawny owls (males: 13 stomachs from the summer and 25 from the winter; females: 39 from the summer and 54 from the winter). Summer represents the period from 15 April to 14 October and winter the period from 15 October to 14 April. (N) represents number of items and (B) the biomass of that item with respect to total biomass.

PREY	REF.	MASS (g)	MALE				FEMALE			
			<i>N</i>	<i>N</i>	SUM	<i>B</i> %	<i>N</i>	<i>N</i>	SUM	<i>B</i> %
			SUMMER	WINTER	(g)		SUMMER	WINTER	(g)	
Mammals										
<i>Clethrionomys glareolus</i>	a	16.00	3	5	128.0	3.27	6	9	240.0	6.14
<i>Microtus agrestis</i>	a	21.00	1	3	84.0	2.15	12	18	630.0	16.11
<i>Sylviaemus flavicollis</i>	a	18.00	2	8	180.0	4.60	15	11	468.0	11.97
<i>Mus musculus</i>	a,b	15.00	1	0	15.0	0.38	0	4	60.0	1.53
<i>Sorex araneus</i>	a,b	10.00	3	2	50.0	1.28	6	5	110.0	2.81
<i>Neomys fodiens</i>	a	10.00	0	0	0.0	0.00	0	1	10.0	0.26
<i>Rattus norvegicus</i>	a	100.00	0	3	300.0	7.67	0	0	0.0	0.00
Unident. voles	g	17.50	3	5	140.0	3.58	5	6	192.5	4.92
Subtotal mammals			13	26	897.0	22.93	44	54	1710.5	43.73
Birds										
<i>Regulus regulus</i>	e	5.30	0	2	10.6	0.27	0	1	5.3	0.14
<i>Turdus merula</i>	e	93.20	0	0	0.0	0.00	1	0	93.2	2.38
Unident. <i>Turdus</i> spp.	f	100.00	1	3	400.0	10.23	2	2	400.0	10.23
Unident. Passeriformes	f	31.00	1	0	31.0	0.79	2	2	124.0	3.17
<i>Glaucidium passerinum</i>	e	60.00	0	1	60.0	1.53	0	1	60.0	1.53
Subtotal birds			2	6	501.6	12.83	5	6	682.5	17.45
Amphibians										
<i>Bufo</i> sp.	h	10.00	1	0	10.0	0.26	0	0	0.0	0.00
Subtotal amphibians			1	0	10.0	0.26	0	0	0.0	0.00
Invertebrates										
<i>Melolontha vulgaris</i>	c	0.92	2 (1) ⁱ	1 (1)	2.8	0.07	0	0	0.0	0.00
<i>Cetonia</i>	h	1.00	1 (1)	0	1.0	0.03	1 (1)	0	1.0	0.03
<i>C. septemunctata</i>	h	0.20	1 (1)	0	0.2	0.01	0	0	0.0	0.00
Coleoptera	c	0.50	0	2 (1)	1.0	0.03	0	1 (1)	0.5	0.01
Saltatoria	h	1.00	0	0	0.0	0.00	2 (2)	1 (1)	3.0	0.08
Lepidoptera	d,h	1.00	3 (1)	4 (2)	7.0	0.18	61 (9)	32 (10)	93.0	2.38
Subtotal invertebrates			7 (4)	7 (4)	12.0	0.31	64 (12)	34 (12)	97.5	2.49

^a Nilsson (1981).
^b Jäderholm (1987).
^c Labes (1990).
^d Linné (1758).
^e Haftorn (1971).
^f Haftorn (1971).
^g Average of the most common four identified mammal species.
^h This study—mass from the stomach analyses.
ⁱ Parenthetical values represent the number of stomachs containing the prey item.

(Temeles 1985). This view is in accordance with our data—males preyed upon relatively large prey (Norway rats and birds) significantly more than did females. Two more aspects imply that there are real differences between the sexes of tawny owls. Firstly, birds may be difficult to catch; hence, it may be risky for the male to specialize on them. This may lead to more empty stomachs in males than in the females, as our data indicate. Secondly, males with prey items in their stomach carried more prey mass than females (37.4 g vs. 29.5 g), despite the larger size of the female. This may imply that when the male is successful the average prey is larger than that of the female. However, most of the sparse sex-specific owl diet data available fails to support the prediction of sexual differ-

ences in feeding niches, perhaps partly because the species studied fed chiefly on voles which provide little variety in size classes (Mikkola 1983, Wiklund and Stigh 1983). The broad diet of the tawny owl, including a large proportion of birds of various sizes, may permit more size partitioning in prey utilization than in some other owl species. In their review, Snyder and Wiley (1976) concluded that RSD in raptors is more likely to be related to advantages conferred on larger females in terms of copulation, incubation, brooding, and nest defense. The advantage of the smaller male, however, may lie in hunting habits (e.g., Earhart and Johnson 1970, Mendelsohn 1986).

Ideally, to test whether males and females select different prey, the diets of pairs which have the same prey available to them should be studied. This would include intensive radiotelemetry studies and sampling of pellets from individual roosting sites, together with close monitoring of density and dynamism in relevant prey species.

RESUMEN.—Verificación del porcentaje de invertebrados en la dieta, así como la posible diferencia entre los sexos con relación a la selección de presa, fue el objetivo durante el análisis del contenido estomacal de 131 cárabos (*Strix aluco*) de Noruega, de sexo conocido y matados accidentalmente. Invertebrados, sobre todo especies de *Lepidoptera*, tales como *Noctua pronuba*, constituyeron el 2.7% de la biomasa total. No se encontró ninguna diferencia entre los sexos con relación a esta parte de la dieta. Generalmente hablando, la biomasa de presa fue dominada por pequeños mamíferos (66.6%) y pájaros (30.2%). Se descubrieron diferencias significantes, debido a que los machos se alimentan relativamente más de los animales más pesados (100 gramos o más), comparado con las hembras, incluyendo en particular la rata parda (*Rattus norvegicus*) y especies de *Turdus*, los cuales representaron un 49% de la dieta de los machos, comparado con un 16% para las hembras, en términos de biomasa. Las hembras obtuvieron el 64% de su alimentación, en términos de peso, de animales de tamaño mediano (15–29 gramos). Animales de este tamaño también formaron una parte importante de la dieta de los machos.

[Traducción de J.R.S. Sciaba]

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A NEW METHOD OF CAPTURING BUTEONINE HAWKS

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Trapping raptors from roads (Watson 1985, Bloom 1987: 103) has been accomplished commonly by using bal-chatri traps (Berger and Mueller 1959), harnessed pigeons (Webster 1976:155), portable phai (Bloom 1987:115), and carrion wrapped with noose carpets (Watson 1985). Although popular, road-trapping by these methods presents several disadvantages: (1) raptors are often wary of "gift-wrapped" food (Bloom 1987:103); (2) harnesses, cages, and monofilament nooses remain visible to target raptors; (3) construction and maintenance of noose traps is time consuming; (4) hawks striking noose traps often do not become entangled (Watson 1985).

To date, trapping raptors with steel leg-hold traps has been aimed almost exclusively at capturing bald (*Haliaeetus leucocephalus*; Harmata 1984) and golden eagles (*Aquila chrysaetos*; Bloom 1987), but leg-hold traps have also been used to capture buteonine hawks (Imler 1937). Herein, we detail our use of leg-hold traps for capturing ferruginous (*Buteo regalis*), red-tailed (*B. jamaicensis*), and Swainson's hawks (*B. swainsoni*) from roads.

METHODS

Use of live bait and padded and weakened leg-hold traps was approved by the University of Minnesota Animal Care Committee prior to initiating this work. Size 3 and

3N double-spring leg-hold traps with offset jaws were used (Oneida Victor Animal Trap Co., Lititz, PA U.S.A.). Traps were greatly weakened by repeatedly striking each spring near the bend with a hammer (Bloom 1987:114), taking care not to misshape springs. Alternately, traps were used that had springs too weak for use as described by Harmata (1984:15) and Bloom (1987:114). Once weakened, traps closed with greatly reduced force and slightly reduced speed. Jaws were first padded with 5-mm-thick adhesive-backed foam rubber, and then wrapped with cloth friction tape. Traps properly weakened and padded still closed quickly, but were capable of being sprung repeatedly on a single human finger without inducing injury or pain. Traps were thoroughly tested in this manner prior to use. The "V" cutout in the trap pan was filled with epoxy for better concealment, and the pan, jaws, and springs were spray-painted either white or brown for use in snow or soil, respectively. No additional weights were used when trapping Swainson's hawks, but a lead weight or short length of chain weighing about 0.3 kg was attached to the trap when used for red-tailed and ferruginous hawks. A wire loop tightened diagonally around the trap base served as a point of attachment for the bait harness (Fig. 1 top).

Deer mice (*Peromyscus* spp.) and domestic laboratory mice (*Mus musculus*) were used as bait. A harness to hold the bait mouse onto the trap pan (Fig. 1 middle) was made as follows: a 24-ga. steel wire was formed into a loop, onto which were threaded the cylindrical portion sawn from a pop-rivet and a leader for attachment to the base of the leg-hold trap. The loop was placed over the head and behind the ears of the mouse, and tightened just enough to prevent escape by the mouse. The cylindrical portion

of the pop-rivet was then flattened using pliers, and the ends of the collar were clipped off. The leader of the harness was passed through a 2-mm hole drilled through the center of the pan, and anchored to the wire around the trap base, providing enough excess for some movement by the mouse. Anchoring the harness to the base of the trap instead of to the pan helped minimize missing birds that attempted to take the bait while in flight, lifting the mouse clear of the closing jaws. Attaching the harness to the trap base maintained the mouse at a consistent height beneath the jaws, independent of the position of the pan.

As with bal-chatris, the trap was placed on the ground from the side of the vehicle opposite the perched hawk to minimize suspicion (Watson 1985). A trap bed was dug for soil sets, but was not needed in snow. Springs were rotated toward the trigger side of the trap, to permit the jaws to lie as flat as possible. Traps were arranged with the springs perpendicular to the hawk's anticipated line of travel, so that the jaws would close on the sides of the leg of the approaching hawk. This was done to lessen the chance of the jaws pushing the hawk's leg clear during closure. A thin covering of snow or sifted soil was used to camouflage the trap. While unnecessary for snow sets, brown polyester batting was used when making sets in soil to help support concealing soil at the height of the pan (Fig. 3 bottom). Once the trap set was completed, vehicles were driven out of sight of the perched hawk, or to a distant point (0.5–1 km) that offered a view of the perched hawk. Traps were left in place for ca. 20 min.

RESULTS AND DISCUSSION

From November 1992 to February 1994, we trapped six red-tailed, ten ferruginous, and seven Swainson's hawks. This technique was also successfully used to retrap three ferruginous and two Swainson's hawks originally captured by this and other methods. This method was most effective when used to capture nesting adult and recently fledged Swainson's hawks, with seven captures from 11 traps set (64%). No nontarget species were captured.

As in the case with bal-chatris, hawks would often approach the trap several times, but not take the bait when the mouse failed to run. However, they often returned or alighted nearby and walked into the trap. Bait mice were either killed by the hawk, or were untouched by the trapped hawk and reused or released. No injuries of any kind were observed on any of the hawks captured by this method.

One disadvantage in our method not inherent in several other forms of road-trapping is that vehicles must be stopped, and often exited, when setting this trap. However, this method offers the advantages of having no components visible to the target raptor, rapid initial construction and set up time, and virtually no maintenance. The importance of properly weakening trap springs, adequately padding trap jaws, and testing the force exerted by the closing trap before use on hawks cannot be overemphasized. This trap is not suitable for species smaller than those mentioned.

RESUMEN.—Una trampa de acero atrapa-patas con un ratón vivo como cebo fue usado para atrapar vivos a individuos de *Buteo jamaicensis*, *Buteo regalis* y *Buteo swainsoni*. La activación de la trampa fue debilitada y sus dientes

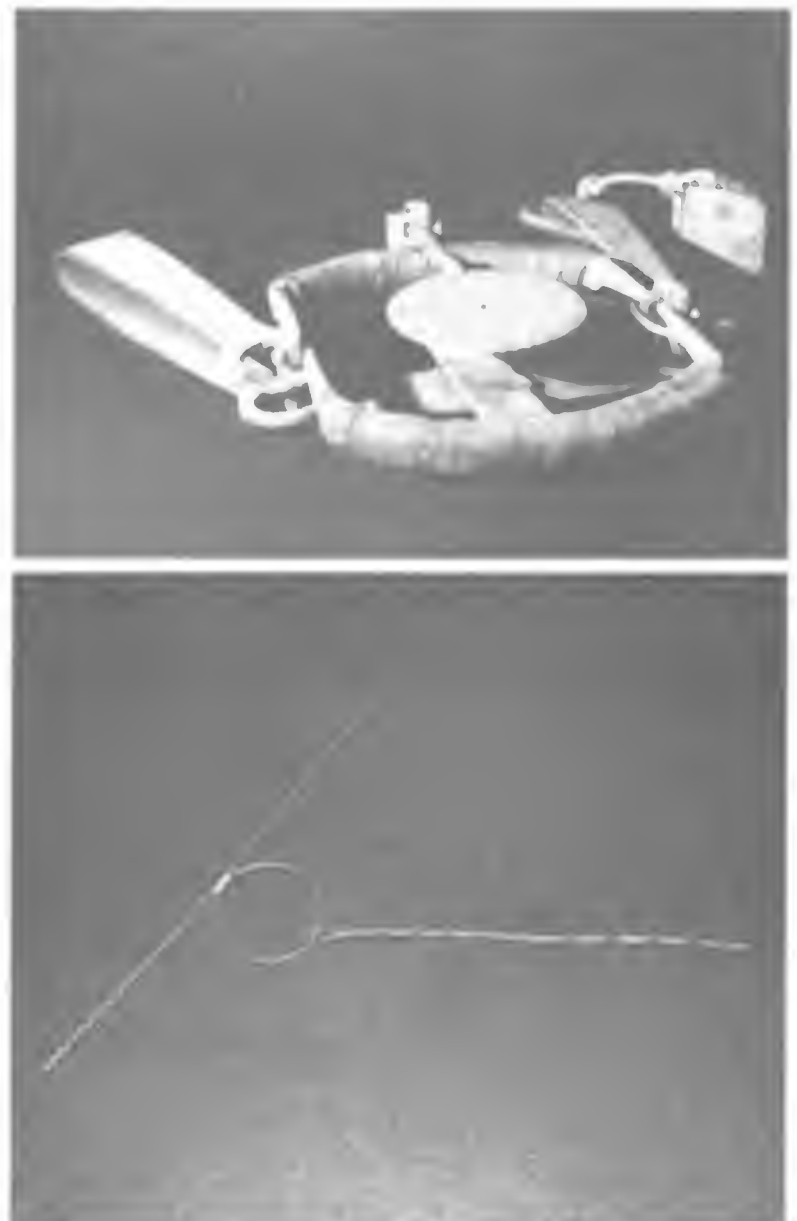


Figure 1. Top: Modified leg-hold trap showing jaw padding and anchor wire around base. Middle: Harness for securing the bait mouse. Bottom: Bait mouse harnessed to the trap and polyester batting.

fuieron forrados para evitar dañar a los aguiluchos. El mayor éxito fue obtenido con *B. swainsoni*, logrando un 64% de los intentos de captura ($N = 11$).

[Traducción de Ivan Lazo]

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LETTER

FISHERMEN AND THEIR GEAR MAY THREATEN BALD EAGLES AT MAGDALENA BAY, B.C.S., MEXICO

The status of the bald eagle (*Haliaeetus leucocephalus*) in Baja California was recently summarized by Henny et al. (1993, *J. Raptor Res.* 27:203–209) who called attention to the critical situation of the only nesting population located in the Magdalena Bay region. They noted that a maximum of only three nesting pairs was found in any year over the last decade, and that the “low numbers and restricted distribution make this disjunct population especially vulnerable to human disturbance.” Although human disturbance may be an important factor influencing the small bald eagle population in the Magdalena Bay region, specific factors affecting this population have not been defined. Here, we present information about two forms of human disturbance of bald eagle nestlings and fledglings in the Magdalena Bay area.

The first type of disturbance is illustrated by an observation that we made on 6 May 1994, while surveying Isla Margarita, Baja California (24°20'–24°31'N, 111°43'–112°01'W) for bald eagles and their nests. We found a fledgling bald eagle suspended in a tree branch. The eagle was alive but entangled with a nylon cord wrapped around its right foot. The pressure of one of the strands of the nylon cord had almost separated the foot from the leg at the tarsometatarsus. We released the bird on a low bush about 1.5 m from the tree.

A bald eagle nest on a big rock, about 300 m from where the fledgling was entangled, was constructed using mainly mangrove tree (*Rizophora mangle*) branches and nylon cord. Nylon cord is used extensively by local fishermen, and therefore, broken strands of nylon cord are present year-round throughout the Magdalena Bay region.

Several studies have shown adverse effects of commercial and recreational fishing activities on raptors (J.M. Meyers 1989, *Ala. Birdlife* 36:17; J.R. Parrish and B.A. Maurer 1991, *J. Raptor Res.* 25:136–139) and marine birds (N. Atkins and B. Henemann 1987, *Am. Birds* 41:1395–1403). Bald eagles elsewhere have been shown to be prone to this danger (J.W. Watson 1989, *J. Raptor Res.* 23:52–53). Poole (1989, *Ospreys*, Cambridge Univ. Press, Cambridge, U.K.) reported that tangled old fishing line in osprey nests sometimes ensnared the young, constricting blood flow and amputating limbs. We have also observed white storks (*Ciconia ciconia*) in Spain lining their nests with plastic cords, and sometimes becoming entangled in them.

The second form of disturbance is the taking of bald eagle fledglings and yearlings as pets by fishermen in Magdalena Bay (E. Amador-Silva and J. Guzman-Poo in press, *Rev. Inv. Cient. UABCS*, La Paz, México). This activity seems to be continuing in the region. A fisherman showed us a picture of a bald eagle fledgling that he took from a nest in 1992 at Puerto Chale. We also have a picture of a first-year bird caught by another fisherman in Lopez Mateos in 1993. Although bald eagles in Magdalena Bay seem to be producing young to the fledging stage at a normal rate (Henny et al. 1993, *J. Raptor Res.* 27:203–209) the population may not be increasing because of the loss of fledglings through entanglement in fishing gear and capture by fishermen.

The Magdalena Bay area now contains the only bald eagle nesting population in Baja California (Henny et al. 1993, *J. Raptor Res.* 27:203–209) and represents the southernmost limit of breeding population for this species. We propose that the Magdalena Bay bald eagle population should be immediately protected to preserve the species in Baja California. Nests should be monitored continuously during the breeding season to prevent the human removal of nestlings. Observers should regularly remove nylon cords from the nests from the time the nestlings are approximately 2 wk old until they fledge. Additionally, fishermen should be targeted for an environmental education program.

We thank C. Blázquez for field assistance and J. Llinas who kindly gave us the pictures of the immature bald eagle from the town of Lopez Mateos. C. Henny and D.W.S. Stahlecker made helpful suggestions on the manuscript. R. Bowers helped with the English translation. Centro de Investigaciones Biológicas del Noroeste and Consejo Nacional de Ciencia y Tecnología gave financial support.—**Ricardo Rodríguez-Estrella, Centro de Investigaciones Biológicas del Noroeste, Division Biología Terrestre, Apartado Postal 128, La Paz 23000 B.C.S., México; José Antonio Donázar and Fernando Hiraldo, Estación Biológica de Doñana, CSIC, Pabellón del Perú, Avenida María Luisa s/n, 41013 Sevilla, Spain.**

COMMENTARY

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ON RAPTOR ROADSIDE SURVEYS IN WESTERN TURKEY AND EASTERN GREECE

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In a recent publication by Eakle (1994), the results of a roadside survey in western Turkey and eastern Greece are detailed. From our point of view the results obtained are scarcely reliable for two reasons: (1) The surveys are very heterogeneous and hardly repeatable. Transects by such different means of transportation as car, train, bus, or on foot are included, with the distances travelled on each of them unspecified (in nine surveys only bus/foot or car/foot are detailed). Obviously, the speed in these cases was not checked by the observer (except when he moved on foot). (2) A possible confusion could occur in the determination of the smaller falcons (genus *Falco*) to the species level. Eurasian kestrels (*Falco tinnunculus*) and lesser kestrels (*Falco naumanni*) amounted to 71.3% of the raptor sightings. We have been intensively working with lesser kestrels for the last 7 yr, including plumage characteristics (see i.e., Negro 1991). We can assert that telling these kestrel species apart in flight is highly problematic even for an expert birdwatcher moving on foot and using binoculars. It is only possible to separate the males of the two species under good light conditions and at close range, and after careful observation (see also Cramp and Simmons 1980). The best way of distinguishing between the species is by their vocalizations. The conditions necessary to distinguish the two kestrel species do not usually occur when observing from a car, and seem impossible when travelling by train or bus. To distinguish flying females is virtually impossible (Porter et al. 1974). In other studies carried out by expert birdwatchers in Mediterranean areas where both species are abundant, the number of undeter-

mined kestrels tends to be high (Meyburg 1973). It is amazing that all of the 132 kestrels observed by Eakle could be identified to the species level. Perhaps the author has assumed that birds in flocks were lesser kestrels and solitary birds were Eurasian kestrels. This would be erroneous. Lesser kestrels are often solitary hunters (authors unpubl. data). Eurasian kestrels are sometimes colonial breeders in Mediterranean farmlands (Porter et al. 1974, Bustamante 1994), and rather often hunt insects in flight, forming monospecific or mixed flocks with lesser kestrels (Negro 1991, authors unpubl. data).

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LESSER KESTRELS OR NOT—A RESPONSE TO HIRALDO ET AL.

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The value and limitations of roadside surveys and abundance indexes for raptors have been well documented (Kochert 1986, Fuller and Mosher 1987, Millsap and LeFranc 1988), and need not be repeated again here. Suffice it to say that most indexes of raptor relative abundance should be used with caution because of variable species detectability and other inherent biases associated with road counts.

Hiraldo et al. (1995) believed that the results of my roadside surveys in Turkey and Greece (Eakle 1994) are unreliable. Their objections were that various modes of transport were used (train, bus, car, and on foot), distances traveled were unspecified, and the difficulty of separating the lesser kestrel (*Falco naumanni*) and Eurasian kestrel (*Falco tinnunculus*).

Contrary to Hiraldo et al.'s first assertion, Table 1 of Eakle (1994) clearly specifies the distance of each survey route. Four surveys were accomplished by train, nine by bus, five on foot, eight by bus and foot, and one by car and foot. The distances for the nine surveys conducted by bus/foot and car/foot were combined, but all foot surveys were less than 15 km and most were 5–10 km in length.

Hiraldo et al. further note that vehicle speeds were not checked during the surveys, an unfortunate circumstance clearly stated in my article. However, vehicle speeds can easily be estimated by knowing the approximate distance traveled and approximate traveling time for each survey—data included in Table 1 of Eakle (1994). For example, the average speed for train surveys was calculated to be 68 km/hr (range 60–81 km/hr); 42 km/hr for bus surveys (range 16–69 km/hr); 1.5 km/hr for foot surveys (range 1–2 km/hr); 12 km/hr for the bus/foot surveys (range 2–30 km/hr); and 8 km/hr for the car/foot survey. For comparative purposes, Donazar et al. (1993) reported driving speeds of 60–70 km/hr during their survey of Argentinean Patagonia, and Ellis et al. (1990) reported speeds of 70–80 km/hr on paved roads and 50 km/hr on unpaved roads during their survey in South America. Andersen and Rongstad (1989) drove at slower speeds of 25–40 km/hr, and Bauer (1982) reported an average speed of 48 km/hr. Therefore, the speeds of the various modes of transport that I used are probably well within the ranges reported by other researchers.

Employing more than one survey method (vehicle type)

is not unprecedented in the literature. Howard et al. (1976) used three survey methods in various combinations in southern Idaho, including ground surveys on foot and with vehicles, as well as fixed-wing and rotary-wing aircraft. Clearly, it is desirable to standardize survey methods when conducting roadside counts, including the type of survey vehicle and driving speeds. However, planning and conducting the surveys in Turkey and Greece presented numerous logistical challenges which were best overcome by employing public transport to the maximum extent practicable. The survey results obviously represent a single count (Bortolotti 1992), but the routes could be repeated by other researchers. Also as noted in Eakle (1994), visibility was outstanding and comparable between trains and buses, and actually seemed superior to viewing opportunities from cars (Eakle unpubl. data).

As mentioned above, Hiraldo et al. (1995) assert that it is extremely difficult if not impossible to distinguish between Eurasian kestrels and lesser kestrels, particularly flying birds and especially females in flight. I wholeheartedly agree that well-developed observational skills and experience are prerequisite to correctly identify these small falcons in the field, particularly when conducting a survey with limited opportunities to stop and identify distant birds. However, despite Hiraldo et al.'s assertion, I found several key field characters useful for distinguishing between these two species—both males and females.

In flight and perched, adult male lesser kestrels are easily distinguished from adult male Eurasian kestrels by the blue-grey panel on the larger wing coverts (Wallace 1983); by the lack of dark spots on the chestnut back (Brown and Amadon 1968, Cade 1982, Steyn 1982, Peterson et al. 1983, Hosking et al. 1987); by the cleaner, whiter underparts with white underwings contrasting with the creamy buff body and black wingtips (Porter et al. 1978, Handrinos and Demetropoulos 1983, Tarboton 1989, Steyn and Arnott 1990); by the lack of moustachial stripes (Porter et al. 1978, Burton 1989); and by the slimmer build, narrower wings, and more slender tail (Wallace 1983, Gensbol 1987).

Adult male Eurasian kestrels show a distinctly spotted back and inner wing (Wallace 1983), and are easily told from adult male lesser kestrels by their black spotted chestnut upperparts, chestnut instead of blue-grey greater co-

verts, flight feathers which are more barred, black moustachial stripe, buffish underparts which are more heavily streaked, and lack of black wing-tips (Porter et al. 1978).

The adult female lesser kestrel is less heavily marked than the adult female Eurasian kestrel (Wallace 1983); has paler and less streaked underparts, especially the underwings and undertail coverts (Cade 1982); is smaller in size (Grossman and Hamlett 1964); and often has a wedge-shaped tail (Porter et al. 1978).

Adult female Eurasian kestrels show heavy moustaches and heavy body streaks (Wallace 1983); are larger in size than lesser kestrels; have more heavily streaked underparts, particularly in the underwing coverts; and clearly have more barring on flight feathers when viewed from below (Porter et al. 1978).

Juvenile lesser kestrels are like adult female lesser kestrels (Cade 1982), and juvenile Eurasian kestrels are like adult female Eurasian kestrels (Tarboton 1989). In the case of juveniles and females, the lesser kestrel has a more pointed tail center than the Eurasian kestrel (Wallace 1983, Gensbol 1987) which is more heavily spotted and streaked on the undersurface (Weick 1980).

As discussed in Eakle (1994), I observed several small flocks of lesser kestrels in Turkey and Greece. Most flocks consisted of six or fewer individuals. However, three larger flocks were observed, composed of nine, 10 and 19 individuals, respectively. The largest flock appeared to be three smaller subgroups, with seven individuals in the largest subgroup. Using the above described field characters, I was able to successfully identify all individuals to the species level. I did not observe any mixed flocks of lesser and Eurasian kestrels during my surveys as mentioned by Hiraldo et al. (1995) and did not make species identifications based on behavior alone as Hiraldo et al. seem to imply.

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BOOK REVIEW

EDITED BY JEFFREY S. MARKS

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Ecology of Boreal Owls in the Northern Rocky Mountains, U.S.A. By Gregory D. Hayward, Patricia H. Hayward, and Edward O. Garton. 1993. *Wildlife Monographs*, No. 124. 59 pp., frontispiece, 6 figures, 19 tables, 1 appendix. ISBN 0084-0173. Paper, \$4.75.—The authors studied habitat choice, diet composition, breeding density, and reproductive success of boreal owls (*Aegolius funereus*; Tengmalm's owl outside North America) in the northern Rocky Mountains, Idaho, U.S.A. from January to August during 1984–88. The study sites were pristine boreal coniferous forests at high elevations (1580–2400 m), where snow depths reach 50–150 cm and snow does not melt until May. Therefore, the living conditions of owls were adverse. I also understood that the working conditions of researchers were harsh, especially in winter and early spring. Considering these environmental restrictions, Hayward et al. have done respectable work. I wonder, though, whether it would have been possible to find study sites with higher owl densities so that the great study effort could have produced more data and more convincing results about breeding parameters.

The best part of the monograph is on the habitat choice of boreal owls, an aspect of the owl's biology that appeared to be very interesting. By far most of the owl breeding (hooting) territories in mountains of Montana, Idaho, and northern Wyoming were located in subalpine fir (*Abies lasiocarpa*) habitats, and no owls were detected below 1290 m elevation. In the authors' study sites, owls bred in mixed-conifer, spruce-fir, Douglas fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) stands. The most common vegetation type in the area, lodgepole pine (*Pinus contorta*) forest, was largely avoided by the owls. Roosting habitat also differed between winter and summer. Winter roost sites were chosen in relation to their availability, whereas summer roosts were in dense forests with greater canopy cover and tree density. Therefore, during summer owls appeared to select sites with a cool microclimate for roosting. The most productive foraging habitat was

found in old spruce-fir stands where prey population densities were also higher. The owls seemed to face conflicting needs in choosing their nesting, foraging, and roosting habitat, and therefore they used large home ranges (\bar{x} = 1450 ha in winter and 1200 ha in summer).

The primary foods of boreal owls were red-backed voles (*Clethrionomys gapperi*), but in winter northern flying squirrels (*Glaucomys sabrinus*) were frequently captured by female owls but not by males. In summer, northern pocket gophers (*Thomomys talpoides*), yellow-pine chipmunks (*Tamias amoenus*) and western jumping mice (*Zapus princeps*) served as most important alternate prey. The dietary separation between sexes in winter was a fascinating observation, and the reader easily sees its implications to the reversed size dimorphism of birds of prey. In Tengmalm's owls, the degree of intersexual size dimorphism is very high in comparison to other European owl species (Korpimäki 1986).

Data on breeding success were limited because the owl breeding density was low and finding nests was not easy. Egg laying did not start until late April to May. This apparently was attributable to difficulties that males had in courtship feeding because of extreme environmental conditions, and that females were slow to gain weight for egg production. Mean clutch size over 5 yr was 3.1 eggs (11 nests during 1984–88), and the mean number of fledglings produced in successful nests was 2.3. Nesting failure rate was high; 10 of 16 nesting attempts failed. All these values are extremely low so that they are only comparable to values of poor vole years in Fennoscandian Tengmalm's owl populations. For example, in my study area in western Finland (63°N), the yearly median laying dates ranged over 44 d (between 14 March and 27 April) and the yearly mean clutch size from 4.0–6.7 during 1973–89 (Korpimäki and Hakkarainen 1991). The data of Hayward et al. suggest that the breeding habitat of the boreal owls they studied was poor, and the reader may be left wondering whether the low breeding parameters recorded also are valid for other North American boreal owl populations.

On the basis of a limited number of radio-tagged

owls, the authors estimated the annual mean adult survival as 46%, but, radiotags may reduce the survival of owls. The wide confidence interval (95% CI = 23-91%) of their estimate may result in a source of error in population growth models where this survival estimate was later used as a central parameter. These models suggested that the study population declined during the 5-yr study. In any case, the authors could have compared their adult survival estimate with Finnish conspecifics and found that their mean estimate appears to be lower than that for Finnish owls. Based on the 281 Finnish band recoveries of Tengmalm's owls found as dead and calculated by maximum likelihood method, the estimates of mean annual survival were 50% (95% CI 43-57%) during the first year of life and 67% (61-75%) thereafter (Korpimäki 1992). Of course, I am well aware that all survival estimates based on band recoveries may include their own shortcomings.

Despite some weaknesses, I find this monograph provides a good basis for further studies on boreal owls in North America. The results probably also serve as the core information for the conservation of this species in North America. I would like to suggest studies on the species in better habitats and in nest boxes where the nests are easier to find and parent

owls could be trapped (although it seems that nest boxes are not accepted to the same degree as in Fennoscandia).

In my opinion, this monograph is enjoyable to read and is of high quality. It should probably belong in the library of any researcher who is studying owls, especially hole-nesting owl species. It is also valuable to all those who are interested in raptors and habitat selection of uncommon species in North America. Therefore, it should be available in most university and other public libraries.—**Erkki Korpimäki, Laboratory of Ecological Zoology, Department of Biology, University of Turku, FIN-20500 Turku, Finland.**

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1995 ANNUAL MEETING

The Raptor Research Foundation, Inc. 1995 annual meeting will be held on 1–4 November at the Duluth Entertainment and Convention Center in Duluth, Minnesota. Details about the meeting and a call for papers will be mailed to Foundation members in the summer, and can be obtained from Dan Varland, Scientific Program Chairperson, Rayonier, Northwest Forest Resources, 413 8th Street, Hoquiam, WA 98550, (telephone 360 538-4582; FAX 360 532-5426; e-mail Daniel.Varland@RAYNR.CCMAIL.COM), and Gerald Niemi, Local Chairperson, Natural Resources Research Institute, University of Minnesota Duluth, Duluth, MN 55811 (telephone 218 720-4279; e-mail GNIEMI@SAGE.NRRI.UMN.EDU). For information about the associated symposium "A Comparison of Forest Raptor Responses to Forest Management—A Holarctic Perspective," contact Gerald Niemi.

RAPTOR RESEARCH FOUNDATION, INC., AWARDS Recognition for Significant Contributions¹

- The **Dean Amadon Award** recognizes an individual who has made significant contributions in the field of systematics or distribution of raptors. Contact: **Dr. Clayton White, 161 WIDB, Department of Zoology, Brigham Young University, Provo, UT 84602 U.S.A.** Deadline August 15.
- The **Tom Cade Award** recognizes an individual who has made significant advances in the area of captive propagation and reintroduction of raptors. Contact: **Dr. Brian Walton, Predatory Bird Research Group, Lower Quarry, University of California, Santa Cruz, CA 95064 U.S.A.** Deadline: August 15.
- The **Fran and Frederick Hamerstrom Award** recognizes an individual who has contributed significantly to the understanding of raptor ecology and natural history. Contact: **Dr. David E. Anderson, Department of Fisheries and Wildlife, 200 Hodson Hall, 1980 Folwell Avenue, University of Minnesota, St. Paul, MN 55108 U.S.A.** Deadline: August 15.

Recognition and Travel Assistance

- The **James R. Koplin Travel Award** is given to a student who is the senior author of the paper to be presented at the meeting for which travel funds are requested. Contact: **Dr. Petra Wood, West Virginia Cooperative Fish and Wildlife Research Unit, P.O. Box 6125, Percival Hall, Room 333, Morgantown, WV 26506-6125 U.S.A.** Deadline: established for conference paper abstracts.
- The **William C. Andersen Memorial Award** is given to the student who presents the best paper at the annual Raptor Research Foundation Meeting. Contact: **Ms. Laurie Goodrich, Hawk Mountain Sanctuary, Rural Route 2, Box 191, Kempton, PA 19529-9449 U.S.A.** Deadline: Deadline established for meeting paper abstracts.

Grants²

- The **Stephen R. Tully Memorial Grant** for \$500 is given to support research, management and conservation of raptors, especially to students and amateurs with limited access to alternative funding. Contact: **Alan Jenkins, George Miksch Sutton Avian Research Center, Inc., P.O. Box 2007, Bartlesville, OK 74005-2007 U.S.A.** Deadline: September 10.
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¹ Nominations should include: (1) the name, title and address of both nominee and nominator, (2) the names of three persons qualified to evaluate the nominee's scientific contribution, (3) a brief (one page) summary of the scientific contribution of the nominee.

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